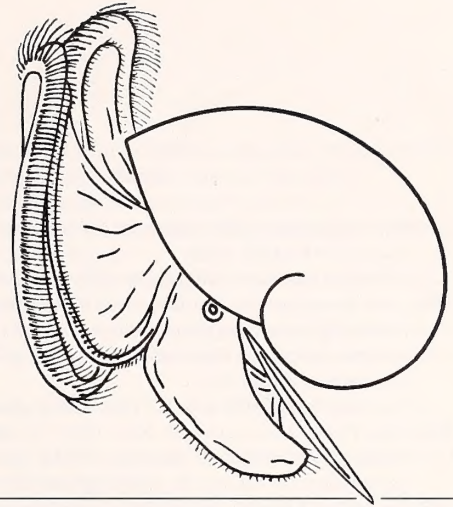


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THE VELIGER

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Volume 42

January 4, 1999 to October 1, 1999

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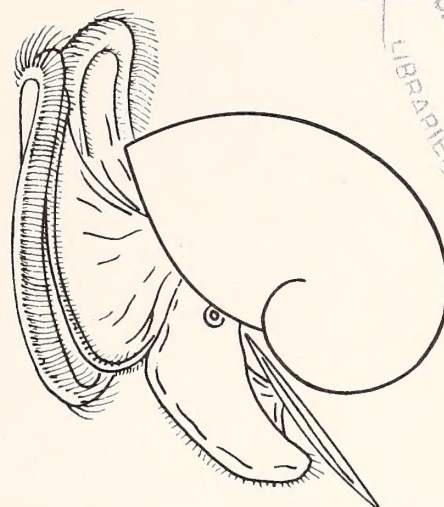
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Very short papers, generally not over 750 words, will be published in a "Notes, Information & News" column; in this column will also appear notices of meetings and other items of interest to our members and subscribers.

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Growth, Seasonality, and Dispersion of a Population of *Aplysia vaccaria* Winkler, 1955

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Abstract. The growth and spatial dispersion of an intertidal population of the California black sea hare, *Aplysia vaccaria* Winkler, 1955, was studied from October 1995 to October 1996 in North Cardiff Beach, California. Population size peaked in November and then declined to zero the following year, while mean weight peaked in June. Breeding was observed throughout the year. The sea hares were spatially clustered and the aggregation pattern was invariant over time. Individual movements and growth were recorded by tagging 19 animals with internal microchips. Tagged animals grew at a rate of 4.9 g/day and moved an average minimum distance of 2.3 m/day.

INTRODUCTION

Intensive research on the neurobiology of sea hares (Kandel, 1979) has been complemented by field studies of their behavior and ecology (e.g., Carefoot, 1967; Usuki, 1970; Kupferman & Carew, 1974; Audesirk, 1979; Nishiwaki et al., 1975; Susswein et al., 1983; Susswein et al., 1984; Carefoot, 1989; Pennings, 1991a, b; Strenth & Blankenship, 1991; Yusa, 1996). One of the least studied of the sea hare species is *Aplysia vaccaria* Winkler, 1955 (Carefoot, 1987). This may be partly due to its perception as "a secretive animal . . . much more difficult to obtain in numbers" than other sea hares (Winkler, 1957). *A. vaccaria* ranges from California to Baja California (Lance, 1967). The species is reported to be primarily nocturnal (Eales, 1960; Pennings, 1991b) and often immobile (Pennings, 1991b), inhabits rocky coasts and kelp beds (Kandel, 1979), spawns in February and March under rocks in shallow water (Winkler, 1955), and feeds upon *Egregia* spp. (Winkler, 1955; Winkler & Dawson, 1963). There are no published data on the growth rate of *A. vaccaria*, its seasonal abundance or its movements in the field (Carefoot, 1987).

In this study, we report on a dense intertidal population of *A. vaccaria* which we were able to monitor regularly for 1 year. Data collected included population size, individual body masses, and fraction of animals mating. The animals in this population appeared to be clustered into small aggregations. *Aplysia* aggregations have often been described (Kupferman & Carew, 1974; Achituv & Susswein, 1985; Pennings, 1991b), but rarely quantitatively, and their function is still unknown. Sea hares may aggregate primarily for mating purposes or other social functions (Susswein et al., 1984; Carefoot, 1987; Pennings, 1991b). On the other hand, aggregations may be caused by differential larval settlement on preferred habitats, at-

traction of adults to patches of food, or attraction of adults to sites with preferred levels of exposure and tidal action (Pennings, 1991a). Because we had the opportunity to map every animal within a fixed study area on each census, we were able to monitor a number of measures of spatial dispersion to see how these changed with season, mean body size, mating frequency, and density of animals. Microchip tagging, a method new to sea hare biology, successfully provided data on growth and movement for a small number of individuals. The result is the first study of dispersion, growth, and survival on this species.

MATERIALS AND METHODS

Site and Study Period

The study population was monitored from October 1995 to October 1996. The site is an intertidal rocky reef at North Cardiff Beach, San Diego County, California (33°1'N, 117°17'W). At the beginning of our study, there was little sand, much exposed bedrock, and extensive cobbling of the upper strand. A year later much of the beach was covered with sand, and most of the tidepools formerly occupied by *A. vaccaria* were covered. We selected a 15 × 19.85 m rectangular census site with deeply eroded channels and pools which harbored high densities of *A. vaccaria*. The tidal range of this site spans from 25 cm above mean low tide level to 90 cm below mean low tide level. The included channels remained filled with water during the lowest tides (-58 cm), and there were many rock ledges under which the sea hares aggregated. Algae in the study site included *Ulva californica*, *Placodium cartilagineum*, *Laurencia sinicola*, *Ceramium* sp., *Pterocladia capillacea*, *Gelidium purpurascens*, *Acrosorium venulosum*, *Jania crassa*, *Herposiphonia* sp., *Centroceras clavulatum*, *Hypnea valentiae*, *Zonaria far-*

lowii, *Dictyopteris undulata*, *Sphacelaria* sp., *Colpomenia sinuosa*, *Egregia menziesii*, and *Macrocyctis pyrifera* drift. The animals in this area were not isolated from human disturbance, although we usually arrived before the low tide and secured cooperation from onlookers in minimizing disturbance to the study site.

Sampling and Mapping Methods

On average, we sampled the site every 2–3 weeks during low tides, which occurred sometime between 4 a.m. and 6 p.m. Each *A. vaccaria* was mapped by recording the distance and compass angle measurement from one corner of the study site to the animal; these were later converted to cartesian coordinates relative to the sides of the study rectangle. Each animal was weighed after removing any debris and as much water as possible from its body. Errors in wet mass measures were estimated by returning five individuals to the water, letting them move about for 5 minutes, and then reweighing them three times. The repeatability (a measure of correlation between repeated measures) of mass measurements was very high ($r = .998$, $SD = 7$ g; Falconer, 1989). Mating status of closely opposed animals was determined by inserting a finger under the parapodia to determine whether or not an everted penis joined individuals.

Density Measures

We used two different measures of density. "Absolute density" is the number of sea hares in the study area divided by the total area in the plot. We also computed an "effective density" by dividing the total number of sea hares counted on a census by the minimum convex polygon required to surround them all. This second density measure thus reflects both the number of animals present and their dispersion.

Dispersion Analysis

The study area was partitioned into 81 contiguous quadrats. Twenty-three of these were considered uninhabitable because of lack of sufficient tidepool area and none ever hosted an animal. All but one of the remaining quadrats did harbor *A. vaccaria* at one time or another during the study. In order to determine whether the animals were significantly aggregated on each census, counts in the habitable 58 quadrats were compared to random (Poisson) expectations with a chi-square goodness-of-fit test.

Where dispersions were significantly non-random, pattern was characterized using several measures of intensity and grain (Pielou, 1969). Intensity measures the difference in sea hare density between cluster peaks and spaces between clusters; grain measures the typical distance between cluster centers and the typical area occupied by a cluster. Lloyd's index of patchiness was an intensity measure computed from quadrat counts. This value indicates

the average number of animals found in the same quadrat with a focal animal after correcting for differences in overall densities. A second measure of intensity was computed by assigning all animals within 1 m of a neighbor to a "cluster" and averaging the resulting number of animals per cluster.

Grain was measured in several ways. The first method was to impose a 10×10 cell grid on the study site and construct correlograms to characterize levels of autocorrelation between numbers of animals/cell at varying cell separations. These plots all showed initial positive autocorrelation (as measured by Moran's I) which dropped to zero and then oscillated around the zero line with increasing cell separations. The farthest separation with a significant positive I (after a Bonferroni correction) and that at which I first crossed the zero line were both noted. The two values are rough estimates of average minimal and maximal cluster size (Upton & Fingleton, 1985). A second measure of grain relied on the number of clusters generated by the 1 m proximity rule: the larger the number of clusters per unit area, the finer the grain. The clustering algorithm also drew minimum convex polygons around each cluster, identified the geometrical centers of the polygons, and computed the enclosed areas. The dispersion of the cluster centers was examined using nearest neighbor methods. The areas of the polygons were used as additional measures of grain: larger mean cluster areas implies coarser pattern grain. Cluster areas could be larger because of more animals per cluster, larger distances between nearest neighbors, or both. To tease apart these effects, we measured average nearest neighbor distances for each census.

Intensity and grain are both likely to vary with population density. We plotted a measure of intensity (the logarithm of cluster size) against a measure of grain (the logarithm of the number of clusters) for successive censuses. Points have to move as overall densities change: which variable shifts least over time can be used as an indicator of the possible mechanisms governing dispersion. Because densities steadily decreased from the fourth census on, we confirmed impressions from the grain vs. intensity plot by regressing the logarithms of animal density, cluster size, and cluster number on time, and then comparing the slopes of the three regressions using ANCOVA.

Finally, we examined the regularity with which different areas in the study site were used by ranking habitable quadrats according to the fraction of the total animals they hosted on each census, and comparing the consistency of quadrat ranks over time using Kendall's index of concordance.

Statistics were undertaken on Macintosh computers using the commercially available Statview and JMP packages. The analyses of intensity and grain were largely undertaken using our own dispersion program called An-

telope (available on the Internet at <http://www-biology.ucsd.edu/research/vehrenbury/programs.html>).

Tagging Methods

Nineteen sea hares were tagged (12 in March and seven in May) using number-coded Trovan passive transponder tags, which were later detected and read with a Trovan LID-500 Hand Held Reader held close to the body of the sea hare. Both the tags and reader were obtained from InfoPet Identification Systems, Inc. Transponder tags, weighing only 0.01% of the weight of a typical individual, were injected under the mantle just inside of the left parapodium. This tagging method was selected for several reasons: we found it to be less likely to attract the attention of curious onlookers than external tags, reducing the human disturbance to the study; tagged animals appeared to be healthy and unaffected by the procedure, and continued to increase in mass, as did the rest of the population; the reader was easy to use and detected microchips quickly, even when wrapped in a plastic bag for protection against moisture.

The 14 tagged animals that were recaptured on subsequent censuses were mapped and weighed. Because our data are limited to those animals that stayed within the study site, and assume a straight line of travel between the two points on subsequent days, our estimates of individual movements are highly conservative. Because we could sample the study area exhaustively, tagged animals not found on one census, but found later, must have emigrated outside the site and then returned. For the census when they were not detected, we recorded the minimum distance between last capture site and the edge of the study area. This is again a conservative estimate of movement over that period given that we routinely searched the immediate area around the study site for tagged animals; hence any sea hares moving out and back into the site must have gone even farther than the value recorded. Mean movement/day was calculated using data from censuses on 5 consecutive days in March (Days 156–160 of the study).

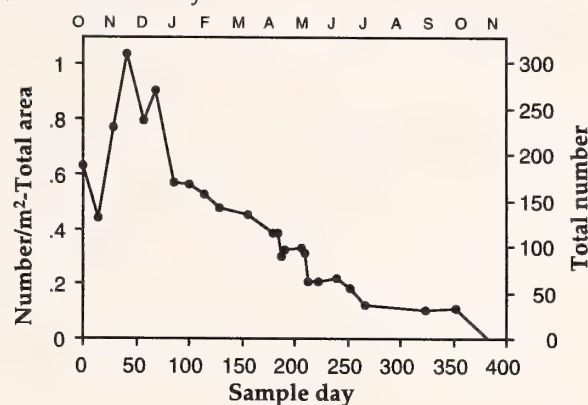
Estimates of short-term movements were obtained by observing 16 animals during four low-tide periods in April (Days 183, 185–187). Each animal was followed for 2 hours between 10 a.m. and 3 p.m., and its location was mapped on a diagram of the study site every 15 min.

RESULTS

Density, Growth and Mating Patterns

The number of sea hares in the study site peaked in November (Day 42) at 310 animals and an absolute density of 1.04 individuals/m²; the corresponding effective density was 1.63 individuals/m². The population then steadily decreased to zero by October of the following year (Figure 1).

a) Absolute density



b) Effective density

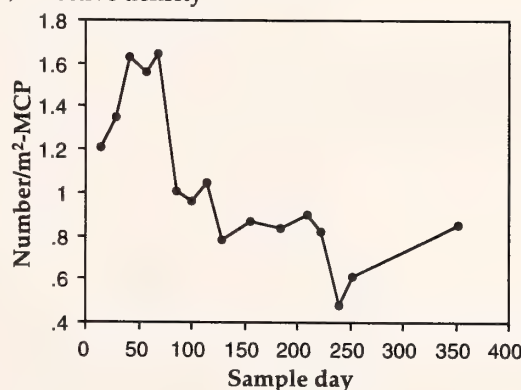


Figure 1

Density of *A. vaccaria* in the study area vs. sample day. a. Absolute density calculated by dividing the number of individuals by the total area of the study site. b. Effective density calculated by dividing the number of individuals by the minimum convex polygon around them (calculated in Antelope). Months are indicated at the top of the figure.

Mean body mass increased in a roughly linear fashion from 372 g in October to the peak of 1105 g in June (Day 239); this corresponds to an average increase of 3.1 g/day (Figure 2). June was also the only time that animals with weights below 180 g were observed; however, these were few in number. The smallest individual found was 30 g. The decrease in mean mass after the June peak was not due to further recruitment of small individuals, but instead to a rapid drop in maximum body size. Because minimal body sizes concurrently increased, this was a period in which the range of body sizes in the site was dramatically reduced.

Body size histories for 13 tagged animals are summarized in Figure 3. All but two samples were taken before the mass peak in June. Although the general trend for the tagged animals is an increase in mass, we observed both rises and falls over the short term. Whether these reflect egg-laying bouts, food shortages, or other constraints on

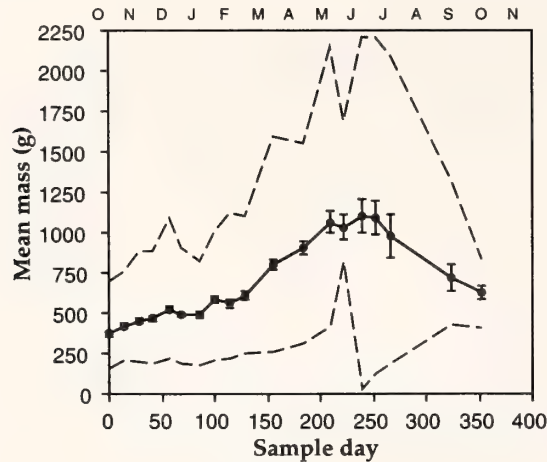


Figure 2

Mean mass of the population vs. sample day (solid line). Bars represent 1.96 standard errors of the mean. Dashed lines indicate maximum and minimum masses for each census. Months are indicated at the top of the figure.

feeding is unknown. Note that some tagged individuals show synchronous increases and decreases in mass, whereas others show quite asynchronous patterns. The average increase in mass for tagged animals was 4.9 g/day over the time period they were followed; this can be compared to a 3.2 g/day average increase in the unmarked population over the same time period. There was a great deal of variance in growth rate ($SD = 8.7$ g, $SE = 2.3$ g) with some tagged animals even losing weight over the period they were monitored. Growth rate of tagged animals was unrelated to their initial weights ($r^2 = 0.02$, $df = 13$, $P > 0.5$). The lower growth rate for the population as a whole during this period when compared to the tagged animals is at least partly due to the appearance of small individuals in the population in June.

In every census, some fraction of the population, between 3% and 43%, was found mating. Both time of day (morning vs. afternoon; Figure 4a) and tide height (Figure 4b) were found to have a significant effect on the fraction of total individuals mating (analysis of covariance on transformed data, $r^2 = 0.51$, $df = 23$, $P = 0.002$). The results indicate that more individuals were mating in the morning censuses ($P = 0.007$) and when the low tide was relatively higher ($P = 0.008$). There was also a significant interaction effect between tide height and time of day on the fraction mating ($P = 0.004$). However, it is impossible to separate the effects of time of day and season, as most of the morning censuses occurred in the spring and summer and most of the afternoon censuses occurred in the fall and winter. Although the number of egg masses was not quantified, newly laid eggs were observed in the study site throughout the entire year's sampling.

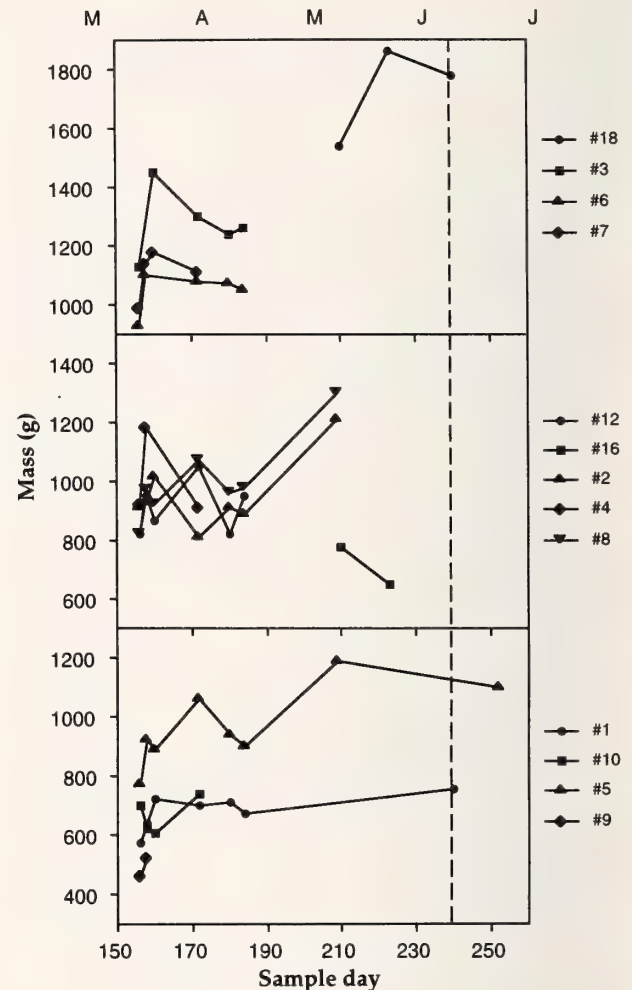


Figure 3

Body size histories for 13 tagged animals which were recaptured and reweighed. Months are indicated at the top of the figure.

Dispersion

Even after uninhabitable quadrats were removed from the analyses, animals were found to be significantly clustered in space on every census (all $\chi^2 > 23$, minimal $df = 3$, and all $P < 0.0001$). Correlograms showed strong positive autocorrelation of animal densities over an average range of 3.4 m, and a drop to zero correlation for quadrats separated by an average 5.3 m (see example in Figure 5). Mean cluster size within a census (using a 1 m linkage rule) ranged from 4.1–12.1 animals/cluster when all individuals were considered, and from 6.2–23.0 when only clusters with more than two individuals were tallied. Mean numbers of clusters in the site ranged from 14–34 including singletons and pairs, and from 8–20 when only clusters larger than two were considered. Clus-

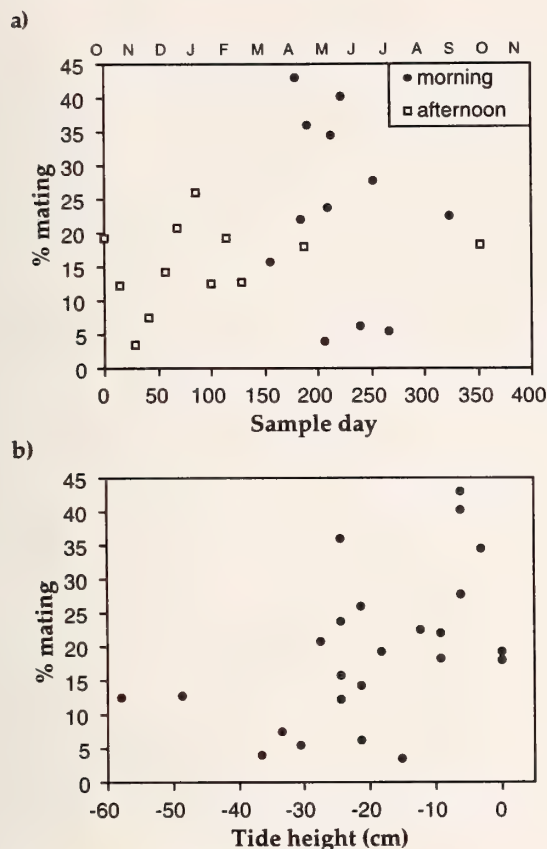


Figure 4

a. Percent of total individuals which were mating in each census. Squares represent afternoon censuses, circles represent morning censuses. Months are indicated at the top of the figure. b. Percent of total individuals which were mating vs. tide height in each census.

ter size and cluster number were uncorrelated ($r = -0.159$, $t = 0.534$, $P > 0.5$).

Population density equals the product of mean cluster size and cluster density. Thus, variation in population density or population size (given the fixed area of our study site) can be completely explained by the independent variations in cluster size and number; whichever of these has the larger variation will dominate variations in density. For our samples, the coefficient of variation in cluster size was 41.4%, whereas it was only 26.6% for cluster number. This suggests that most of the variation in density was due to changes in cluster size. This is confirmed in Figure 6a, which summarizes how mean cluster size and number each varied as population size decreased over time. The relative stability of cluster number when compared to cluster size is demonstrated statistically in Figure 6b. Here, the logarithms of density, cluster size, and cluster number are regressed against sample date over the period of population decline. The regres-

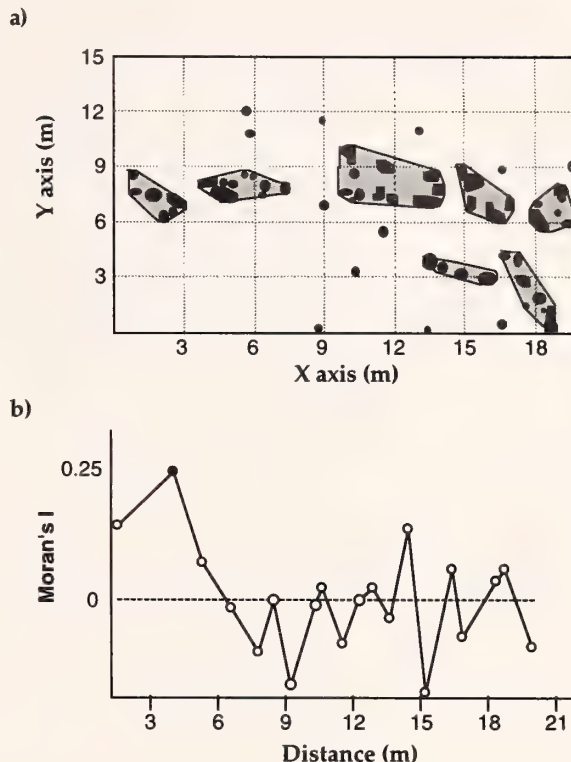


Figure 5

a. Dispersion and size of clusters using 30 cm linkage rule (dark stipple) and 1 m linkage rule (light stipple) for census on 19 December 1995 (Day 69). A total of 270 animals were recorded on this census. b. Correlogram based on a 10×10 grid for above sample. Dark circle at distance of 3.75 m corresponds to Moran's I of 0.241 ($P = 0.00275$). This is just slightly greater than the $P = 0.0025$ required by a Bonferroni correction given an overall significance level of 0.05 and 20 tests.

sions show a rate of drop in number of clusters which is significantly slower than that for cluster size or overall density, but statistically similar rates for drops in cluster size and population density. This again suggests that density decreases were accomplished as reductions in numbers of animals/cluster, not in the number of clusters. This linkage between density and cluster size is also indicated by a plot of Lloyd's index of patchiness vs. sample day (Figure 6c). There is no significant trend here indicating that once variations in density have been taken into account (a fundamental focus of this index), the intensity of the spatial pattern is invariant over time.

The area of clusters as measured by the 1 m clustering rule is negatively correlated with sample day ($r^2 = 0.735$, $P = 0.0002$). Since it is also positively correlated with mean cluster size ($\ln(\text{cluster area}) = 2.1 \ln(\text{cluster size}) - 5.3$; $r^2 = 0.871$, $P = 0.0001$), the decrease in cluster area could simply reflect the demonstrated drop in mean cluster sizes over the season. However, the 2.1 coefficient

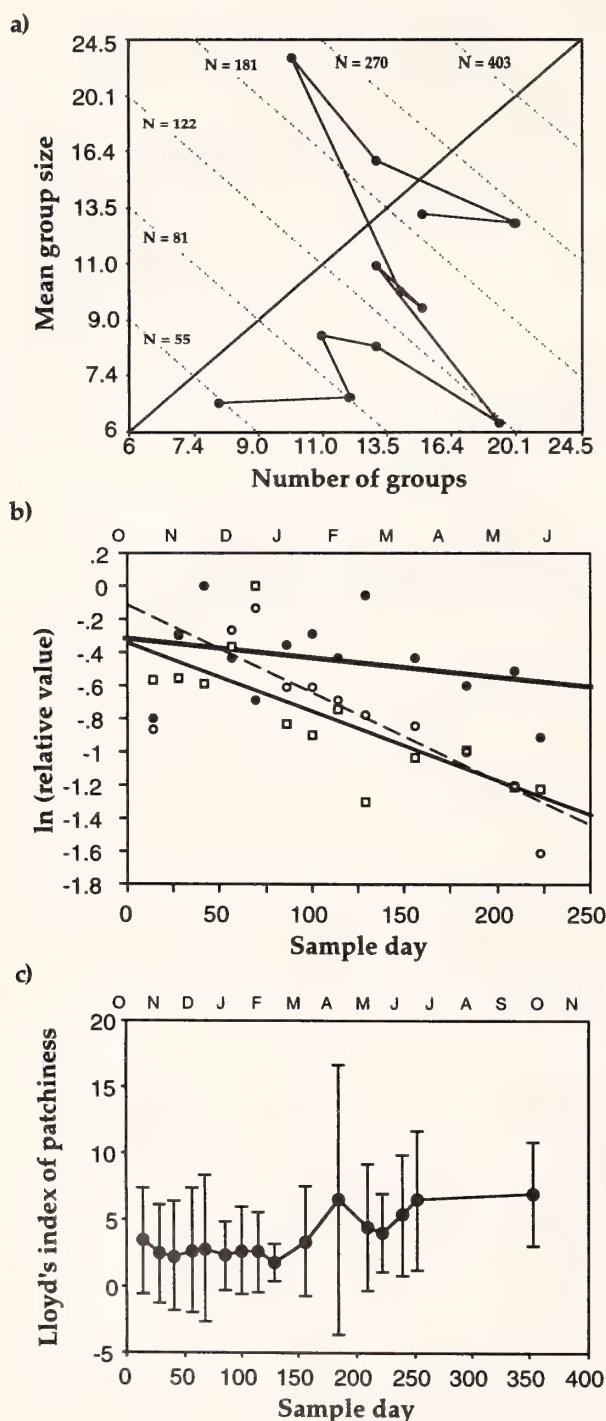


Figure 6

a. Mean cluster size vs. number of clusters for successive censuses after population peak. Clustering uses 1 m rule and only shows groups greater than two individuals. Note logarithmic axes which cause isopleths of equal density to plot as straight lines with a slope of negative one (dotted lines with selected densities indicated). As density decreases, points must move closer to low-

in the log-log regression implies that cluster area depends upon the square of the number of animals in a cluster. Were each animal to require the same amount of space around it, and animals settled in clusters with efficient packing, cluster area should depend only on the first power of cluster size. A likely explanation is that the area added to a cluster per animal is not a constant. In fact, a regression of area/cluster member vs. sample date shows a highly significant decrease over the season ($r^2 = 0.684$, $P = 0.0005$). This could arise either because individuals crowd more closely together later in the season, or because they do not pack into clusters efficiently. Mean nearest neighbor distances range from 14–25 cm, but show no seasonal effects ($r^2 = 0.035$, $P = 0.542$). Thus, the answer is not variation in individual spacing. Because the animals tend to aggregate around the margins of large boulders, their within-cluster dispersion is often curvilinear. This could easily increase the area of enclosing polygons at rates faster than were animals to pack in a contiguous fashion.

If the 58 habitable quadrats are ranked according to the fraction of animals they harbor on each census, there is a high degree of repeatability in quadrat rank over the season (Kendall's index of concordance, $\chi^2 = 249$, $df = 56$, $P < 0.0001$). In fact, the same 17.5% of the quadrats host an average 48% (95% CL = 40–56%) of the animals on any census, and of these, the top 9% harbor an average 24% (CL = 18–30%) of the population.

Individual Movements

Minimum values for the cumulative distances traveled since first capture date are shown in Figure 7a. A conservative estimate of the minimum mean distance traveled per day by 11 tagged animals on 5 subsequent days is 2.3 m/day ($n = 42$, $SE = 0.3$). Eleven of the 42 dis-

er left corner of graph. Diagonal from upper right to lower left indicates trajectory points would follow were decreases in density accommodated by equivalent decreases in cluster size and cluster number. The fact that most points are below this diagonal indicates that drops in density are largely borne by drops in cluster size; cluster number remained relatively stable over the study period. b. Rates of seasonal decrease in overall density of animals on the study plot (open circles and dashed line), numbers of clusters (filled circles and dark solid line), and mean cluster sizes (squares and thin solid line). All measures normalized by dividing by maximum value for season and transformed using logarithms. Results of ANCOVA indicate a significant overall effect of sample day ($F_{2,29} = 44.1$, $P = 0.0001$) and measure ($F_{1,29} = 7.8$, $P = 0.0001$). Post hoc tests using both Fisher's LSD and Scheffe tests indicate significant differences in slopes of density vs. number of clusters ($P = 0.014$ and $P = 0.046$ respectively), and cluster size vs. number of clusters ($P = 0.0006$ and 0.0024), but not between density and cluster size ($P = 0.222$ and 0.478). c. Lloyd's index of patchiness over time. Bars represent 1.96 standard errors of the mean.

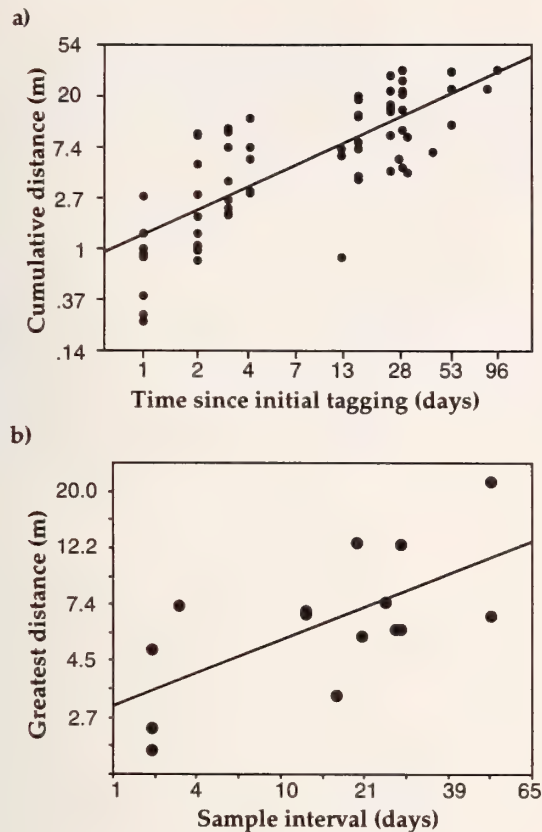


Figure 7

a. Conservative estimates for cumulative distance traveled by each of the tagged animals over the time that they were recaptured. Regression equation is $\ln(\text{cumulative distance}) = 0.28 + .70 \ln(\text{time})$ ($r^2 = 0.57$, $df = 69$, $P < 0.0001$). b. Distance between two most distal capture locations vs. time interval between capture events for each of the tagged animals. Regression equation is $\ln(\text{max distance}) = 0.53 + 0.58 \text{ time}^{0.3}$ ($r^2 = 0.43$, $df = 14$, $P = 0.0078$).

tance measurements are based on estimates of the minimum distance traveled by animals leaving or returning to the study site, and two values are missing because the animals left the study site, but did not return on the consecutive days. Figure 7b shows the greatest distance between two recapture sites for each tagged animal as a function of the time interval between the corresponding recaptures. Maximum distances between recapture sites range from 3–12 m and increase significantly with the interval between recaptures. Direct observations of individual movements during low-tide periods indicate that *A. vaccaria* move an average of 0.92 m/hour ($SD = 1.4$, $SE = 0.24$), and that movement is restricted when the tide is especially low (ANOVA, mean for -3 cm and -6 cm tides = 1.5 m/hr, mean for -12 cm tides = 0.5 m/hr, $p = 0.04$). During these observation periods, sea hares were seen grazing on *Ulva*, smaller red and brown algae

on the sides of rock ledges, and drifting pieces of *Macrocystis* and *Egria* trapped in deep tidal pools.

DISCUSSION

Most sea hares are thought to have maximum life cycles of 1 year (Miller, 1960; Carefoot, 1967; Audesirk, 1979; Carefoot, 1987; Strenth & Blankenship, 1991). While we were unable to follow tagged individuals for their full lifetime, the temporally changing weight distribution for the population does not contradict the possibility of a year-long life cycle for *A. vaccaria*. If we assume that the mean weight of the population was increasing at the same rate before this study as during the increasing portion of this study, the estimated recruitment time of this population would have been June–July, 1995. This, in combination with the presence of small individuals in June 1996, indicates a late spring or summer recruitment time for *A. vaccaria*. There is evidence of some overlapping of generations, as small animals were present with the largest individuals in June. The scarcity of small animals and absence of juveniles smaller than 30 g may reflect a low recruitment rate for the year of this study, or may indicate that juveniles recruit to other locations or habitat types. The increase in amount of sand within the study site was not quantified, but may have contributed to the decline of the population. Very few dead animals were found during the last censuses, and these were quickly washed offshore. It is important to note that because this study population was not a closed one, the measured changes in density and mass cannot be entirely attributed to the seasonal patterns of settlement, growth, and death, but could also be caused by migration into and out of the site.

A. vaccaria is described as the largest gastropod in the world with record sizes of 14 kg and 99 cm (Behrens, 1991). To attain such large body sizes in 1 or 2 years would require a rapid growth rate. While both population averages and tagged animals showed rapid growth, individuals in this study did not approach these record sizes. There are several possible explanations for the large difference in body sizes between record animals and those in this study: there may be greater variance in lifespan than what is seen in most sea hares, such that record animals live longer than 1 or 2 years; the study site may be a marginal or lower quality habitat for *A. vaccaria*; while there was sufficient food in the site to attract and support growth for record densities of these animals, it may not have been the amount or quality required for record growth rates in such a dense population. Our observations show that the *A. vaccaria* diet is considerably broader than suggested by Winkler & Dawson (1963).

The data on individual movements support the claim that the activity of intertidal sea hares is often restricted during extremely low tides due to exposure to the air (Kupferman & Carew, 1974; Carefoot, 1987). Our finding

that members of this population are less likely to mate during the lowest low tides may be explained by the fact that many animals were partially exposed. The resulting reduction in movement is likely to reduce encounter rates with potential mates, and dessication may make it physically difficult for sea hares to mate. The significantly higher levels of mating in the morning censuses of April, May, and June might be explained by time of day, season, or both. If *A. vaccaria* are indeed nocturnal (Eales, 1960; Pennings, 1991b), they may initiate mating during the night and then continue on into the morning. It is also possible that they mate more in the spring, allowing for high levels of recruitment in the summer. In any case, it is clear that *A. vaccaria* are not limited to reproducing in February and March (Winkler, 1955), but spawn year-round.

The dispersion data show that, like other sea hares, *A. vaccaria* is characterized by dense aggregations, and that as densities vary seasonally, the number and spacing of clusters is strongly conserved. This could arise because the animals are willing to travel a limited distance to join a cluster, and thus the spacing of clusters depends only on the area of the site and this typical range, or it could arise because there are favored locations in which clusters might form. The consistency in location of clusters supports the latter possibility. Pennings (1991b) noted that aggregations of *A. californica* often appeared in the same locations as previous aggregations, indicating a preference for certain sites, either because those sites are more environmentally suitable or because they were previously occupied, leaving olfactory cues as a basis for subsequent aggregations. Our data indicate that this site-fidelity is also true for *A. vaccaria*.

Microchip tagging of individuals showed that they moved across an average of 6 m of the study site during the 2 weeks between censuses (as indicated by the greatest distances between recapture locations), and some moved completely across or even out of the 15 × 19.85 m study site. The minimum average daily movements of 2 m were themselves as great as the typical distances between clusters (about 1–3 m). Average hourly movements of 0.92 m also allowed for a great deal of movement between clusters, even during low tides. Tagged individuals were found in different clusters in subsequent recaptures, and the sizes of clusters varied above and beyond global density changes. All of these results suggest that the dispersion patterns are not simply the consequence of initially patchy recruitment of larvae, but rather that these very mobile animals are actively aggregating. Given normal movements, each animal thus has a choice of many groups that it could join.

An earlier study (Winkler, 1955) suggested that reproduction in *A. vaccaria* was limited to a few winter months. The fact that the animals aggregate year-round could then have been construed as evidence against clustering as a mating strategy. Our data show clearly that clustering and

breeding are both maintained year-round, normal ranging allows access to multiple clusters, and most clusters contain mating animals. It thus remains possible that clustering in *A. vaccaria* is related to mating strategies as has been suggested for other members of the genus (Audesirk, 1979; Carefoot, 1987; Pennings, 1991b).

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Metazoan Parasites and Pearls in Coexisting Mussel Species: *Mytilus californianus*, *Mytilus galloprovincialis*, and *Septifer bifurcatus*, from an Exposed Rocky Shore in Baja California, Northwestern Mexico

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Abstract. Metazoan parasites, *Modiolicola gracilis* Wilson (Copepoda), *Pseudomyicola spinosus* Rafaelle & Monticelli (Copepoda), *Urastoma cyprinae* Graff (Platyhelminthes), unidentified encysted trematode cercaria, and pearls were found in coexisting mussel species: *Mytilus californianus* Conrad, *Mytilus galloprovincialis* Lamarck, and *Septifer bifurcatus* (Conrad) from the upper intertidal zone of an exposed rocky shore in Baja California, northwestern Mexico. Incidence of parasites and pearls was greater in *M. californianus*, the largest species of mussels examined, than in the other mytilids. The lowest incidence of parasites and pearls was in *S. bifurcatus*, the smallest species of mussels examined. The highest parasite prevalence coincided with the autumn and winter months when *M. californianus* and *M. galloprovincialis* had a lower condition index and were reproductively active. All parasites produced histological alterations in their hosts; a hemocytic reaction and compression of tissues were commonly observed. In spite of *M. californianus* being the most parasitized species, it is the dominant component in the upper intertidal zone. These results suggest that factors specific to the infesting metazoan parasites in *M. galloprovincialis* and *S. bifurcatus* reduce their competitiveness capacity against *M. californianus*.

INTRODUCTION

The exposed rocky intertidal component of Pacific Northwest shorelines is dominated by structurally complex beds of the intertidal mussel *Mytilus californianus* Conrad, 1837 (Suchanek, 1992). In mussel beds in California, *M. californianus* may coexist with *Mytilus galloprovincialis* Lamarck, 1819 (after the works of Harger [1972a, b] in Santa Barbara, California, the dominant *Mytilus edulis*-like species in southern California were indentified as *M. galloprovincialis* [see McDonald & Koehn, 1988; Koehn, 1991]), and *Septifer bifurcatus* (Conrad, 1837) (Harger, 1972a, b; Haderlie & Abbott, 1980). On the exposed rocky shores of Baja California, northwestern Mexico, the three species also coexist. *Mytilus californianus* is dominant in the middle intertidal zone where it forms a relatively uniform carpet. However, in the upper intertidal zone, *M. californianus* coexists with aggregations of *S. bifurcatus* and *M. galloprovincialis*. The latter may be found in clumps or may be scattered singly in tidepools. There are a variety of studies on distribution, competition, and ecology in mixed populations of *M. galloprovincialis* and *M. californianus* on the Pacific coast of California

(Harger 1968, 1970, 1972a, 1972b; Petraits, 1978; Suchanek, 1978; Witman & Suchanek, 1984). However, studies on the relationships among the coexisting mytilids, *Mytilus* spp. and *Septifer* spp. (Haas, 1942; Hoshiai, 1964) and on parasites of coexisting *Mytilus* spp. (Cous-tau et al., 1990) are scarce.

No studies exist on the interaction of coexisting mytilids, *M. californianus*, *M. galloprovincialis*, and *S. bifurcatus* and their parasitic load. However, that interaction may be important from an ecological and epizootiological point of view. Suchanek (1992) showed the extreme biodiversity associated with *Mytilus californianus* beds in southern California. Over 300 species of plants and animals live within the layers and spaces of these mussel beds, one of the most diverse temperate communities described. Several of these species have been considered as ecto-symbionts (Laihonen & Furman, 1986). There is no information about the diversity of metazoan parasites affecting coexisting mytilids at the same time period in spite of the fact that *Mytilus* species may be infested by more than 50 kinds of organisms (Lauckner, 1983). Pearl formation in mussels has been associated with the presence of trematode cysts and has been considered as an abnormality (Lutz, 1980; Lauckner, 1983). Consequently, their presence may be considered as a part of the parasitic load in mussels. The aims of the present work were to determine the diversity of metazoan parasites and pearls associated with the soft body of *M. californianus*, *M. gal-*

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loprovincialis, and *Septifer bifurcatus* that coexist in the upper intertidal zone of an exposed rocky shore in Baja California northwestern Mexico, to corroborate histologic damage, and to discuss relationships among metazoan parasites and pearls and their hosts.

MATERIALS AND METHODS

From August 1995 to July 1996, 30 adults of the blue mussel *Mytilus galloprovincialis* (mean total shell length 44.20 mm, SD = 7.25), the Californian mussel *Mytilus californianus* (mean total shell length 63.61 mm, SD = 4.23), and the branch-ribbed mussel *Septifer bifurcatus* (mean total shell length 34.65 mm, SD = 3.11 mm) were collected each month from the upper intertidal exposed rocky shore of La Mina del Fraile (31°19'N, 116°26'W) Baja California, Mexico, where the three mussel species coexist.

After removal of any fouling organisms, each mussel was measured (total shell length) and weighed (total weight), and then placed in a Petri dish and opened. Intervalvar water and mussel flesh were examined for the presence of parasites under a dissecting microscope. Parasites and cysts were picked up with a dissecting tweezers from the gills and mantle, and all pearls were removed from the space between the mantle and the inner shell. Turbellarians were preserved in Steinmann's fluid (1 part concentrated nitric acid, 1 part saturated solution of mercuric chloride in 5% sodium chloride, 1 part distilled water) (Sluys, 1989). Copepods were preserved in 70% ethanol. Pearls were dried and stored in glass vials. Cysts were excised with a bistoury under a dissecting microscope to extract metacercaria and were preserved in 70% ethanol. The following works were used for metazoan identification: Graff 1913; Raffaele & Monticelli, 1885; Ho, 1980; Lauckner, 1983; Do et al., 1984; Do & Kajihara, 1986.

Total weight (TW), wet meat weight (MW), and shell weight (SW) of mussels were recorded to obtain a condition index where $CI = [MW/(TW - SW)] \times 100$ (Aguirre, 1979). Parasite prevalence was estimated as the number of infested mussels/number of mussels examined $\times 100$.

Sixty mussels were used for histopathological evaluation; in this case, parasites were not picked out. The soft body of these mussels was removed from the shell and fixed whole in Davison's fixative (Shaw & Battle, 1957) for at least 24 hr. An anterior transverse section including digestive gland, mantle, and gills was taken. Tissue samples were embedded in paraffin wax and were sectioned at intervals of 5 μ m; histological sections were stained with hematoxylin and eosin (Shaw & Battle, 1957). Tissue analysis and measurements were made with a micrometer eyepiece placed in an optical microscope (Olympus BH-2).

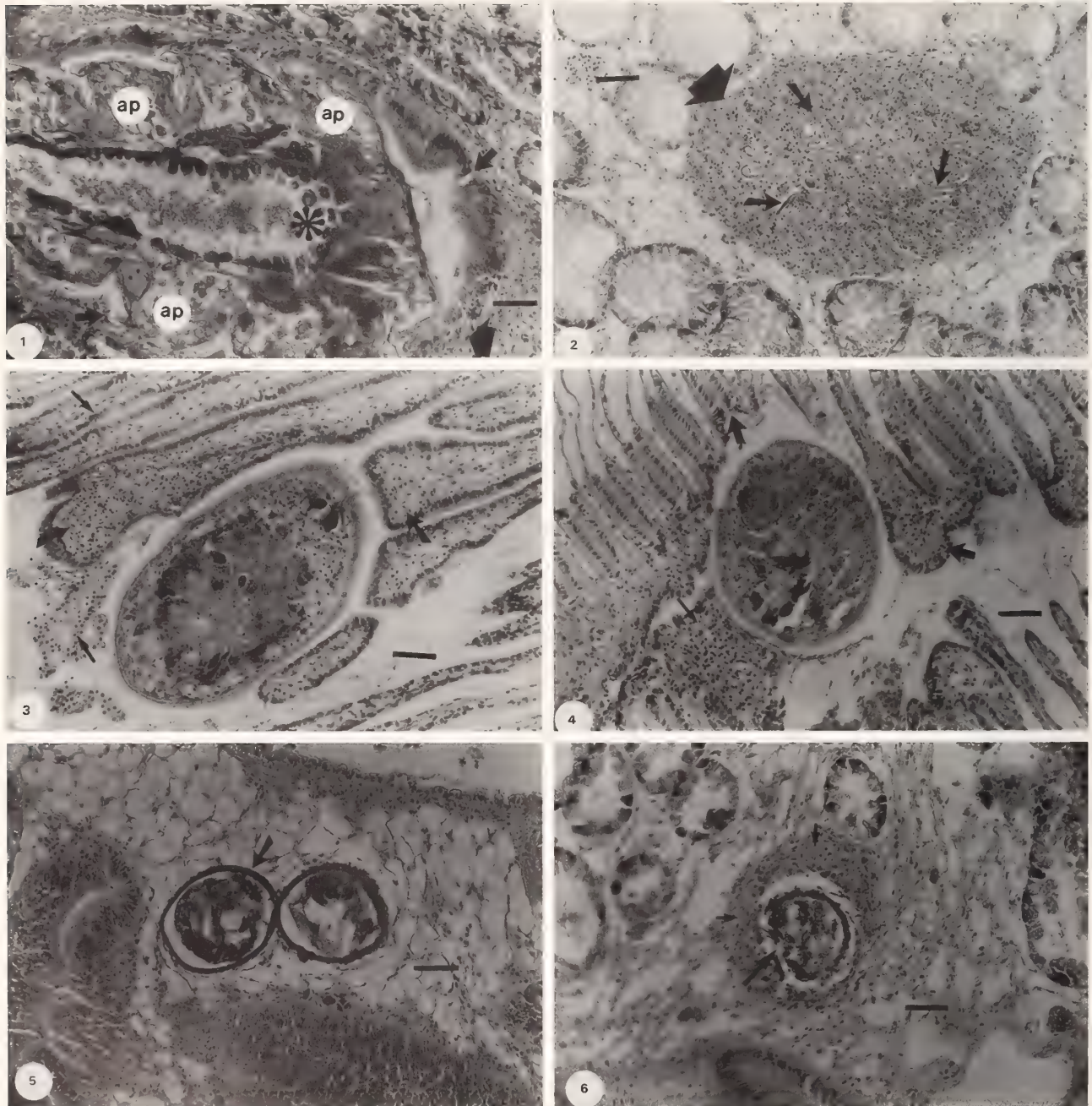
A Kruskal-Wallis test was used to compare the preva-

lence of parasites among mussel species, and one way ANOVA followed by a mean comparison test SNK was used to compare the CI and prevalence of parasites in different mussel species.

RESULTS

The same species of metazoan parasites were found in *Mytilus californianus*, *Mytilus galloprovincialis*, and *Septifer bifurcatus*. They were identified as: *Pseudomyicola spinosus* (Raffaele & Monticelli, 1885) (Copepoda, Mycolidae) (specimens deposited in the United States National Museum, Smithsonian Institution, USNM 274221; *Modiolicola gracilis* (Wilson, 1935) (Copepoda, Clausidiidae), (USNM 274222; *Urastoma cyprinae* (Graff, 1913) Platyhelminthes, Urastomidae) (specimens deposited in the Zoological Museum Amsterdam, V.Pl. 899 and Vpl. 900) (detailed morphological features of these species have been shown by Cáceres-Martínez et al., 1996a, b; Cáceres-Martínez & Vásquez-Yeomans, in press); and unidentified trematode encysted metacercaria, probably genus *Himasthla* (see Lauckner, 1983). This is the first record of these parasitic copepods and turbellarians in *S. bifurcatus*. Both copepod species were found crawling on gills and mantle; the turbellarians were observed among gill filaments and crawling on the gills where some decoloration was found. Encysted metacercaria were observed in the base of the gills and labial palps. Pearls of different sizes were found between the mantle and internal surface of the shell in the three mussel species studied.

Histopathological analysis revealed that both copepod species may be found inside the digestive tract. Identification was possible due to the characteristic body shape of both copepod species. The prosome of *P. spinosus* is more slender than the prosome of *M. gracilis* (see figures in Cáceres-Martínez & Vásquez-Yeomans (1997) for the former, and Do & Kajihara (1986) for the latter). Although *Mytilicola orientalis* has been found in mussels from the Pacific coast of North America (Lauckner, 1983), its modified body is easily distinguishable from the copepods here reported and we did not find evidence of this species in the present study. There was no damage observed in the gills, only compression of gill filaments, but in the gut and stomach, appendages of *M. gracilis* and *P. spinosus* caused erosion of the epithelium and a hemocytic reaction (Figure 1). Some copepods were found within the connective tissue of the digestive gland where a strong hemocytic reaction (encapsulation) was observed (Figure 2). *Urastoma cyprinae* produced a compression, erosion, and rupture of gill filaments and a hemocytic reaction (Figures 3, 4). Encysted metacercaria may or may not produce a hemocytic reaction from the host. They were observed in gills, labial palps, and connective tissue of the digestive gland and mantle (Figures 5, 6).



Explanation of Figures 1 to 6

Figure 1. *Modiolicola gracilis* in the gut of *Mytilus californianus*. Asterisk shows the copepod body, ap = copepod appendages. Thin arrows show the eroded epithelium of the gut and the wide arrow shows the completely destroyed epithelium and hemocytic reaction of the host in this area. Copepod may obstruct the gut. Scale bar = 50 μ m. Figure 2. Granulocytoma in *Mytilus californianus*. Hemocytes are engulfing the copepod found within in the connective tissue of the digestive gland. Large arrow shows the granulocytoma and the small arrows show appendages of the encapsulated copepod. Scale bar = 50 μ m. Figure 3. *Urastoma cyprinae* in the gills of *Mytilus galloprovincialis*. Presence of the worm results in accumulation of hemocytes in gill filaments around the worm (large arrows), gill filament compression (thin arrow at the top), and small clusters of hemocytes around the turbellarian; these hemocytes appear to have ruptured from the gill filaments (thin arrow). Scale bar = 50 μ m. Figure 4. *Urastoma cyprinae* in the gills of *Mytilus californianus*. As with *Mytilus galloprovincialis*, the presence of the turbellarian is characterized by swelling of the gill filaments. See hemocyte accumulation in gill filaments around the worm (big

Table 1

Minimum and maximum number of parasites (range) per mussel species observed from August 1995 to July 1996.

Month	<i>Septifer bifurcatus</i>				<i>Mytilus galloprovincialis</i>				<i>Mytilus californianus</i>			
	<i>Urastoma cyprinae</i>	<i>Modioli-cola gracilis</i>	Trematode cysts	Pearls	<i>Urastoma cyprinae</i>	<i>Modioli-cola gracilis</i>	Trematode cysts	Pearls	<i>Urastoma cyprinae</i>	<i>Modioli-cola gracilis</i>	Trematode cysts	Pearls
A	0-0	0-0	0-0	0-0	0-2	0-0	0-0	0-0	0-11	0-0	0-0	0-3
S	0-1	0-1	0-0	0-0	0-2	0-2	0-0	0-1	0-9	0-1	0-0	0-4
O	0-1	0-1	0-0	0-0	0-1	0-4	0-1	0-3	0-7	0-15	0-1	0-4
N	0-0	0-2	0-0	0-0	0-3	0-1	0-0	0-0	0-6	0-8	0-0	0-4
D	0-1	0-2	0-0	0-0	0-8	0-5	0-0	0-5	0-38	0-10	0-0	0-1
J	0-0	0-1	0-0	0-0	0-20	0-1	0-0	0-0	0-34	0-7	0-1	0-7
F	0-0	0-2	0-0	0-0	0-18	0-5	0-1	0-0	0-23	0-9	0-1	0-3
M	0-0	0-1	0-0	0-0	0-4	0-2	0-0	0-0	0-38	0-5	0-0	0-0
A	0-0	0-0	0-1	0-1	0-42	0-0	0-0	0-0	0-95	0-2	0-0	0-1
M	0-0	0-0	0-0	0-0	0-3	0-3	0-7	0-2	0-2	0-0	0-0	0-1
J	0-0	0-0	0-0	0-0	0-1	0-0	0-0	0-3	0-5	0-0	0-0	0-0
J	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-0	0-2	0-0	0-2	0-0

Table 1 shows the range of parasites and pearls in mussels, and Figure 7 shows their prevalence. *Urastoma cyprinae* was the most abundant parasite in *M. californianus* and *M. galloprovincialis*, its number ranged from 0 to 95 in the former and from 0 to 42 in the latter. Their maximum prevalence occurred during autumn-winter, and prevalence was similar in *M. californianus* and *M. galloprovincialis* but different in *S. bifurcatus* (Kruskal-Wallis Test, $H = 2.25$, $P < 0.001$, followed by SNK method, $q = 2.5$, ns). In *S. bifurcatus* the number of *U. cyprinae* ranged from 0 to 1 and prevalence was minimum and occurred in September, October, and December 1995. *Modiolicola gracilis* was also abundant, its number ranged from 0 to 15 in *M. californianus* and from 0 to 5 in *M. galloprovincialis*; its prevalence was similar in both hosts (Kruskal-Wallis Test, $H = 4.77$, $P = 0.09$). This copepod was found ranging from 0 to 2 individuals in *S. bifurcatus*, and it was only observed during autumn-winter. Two *Pseudomyicola spinosus* were found in *M. californianus*; only one was observed in *M. galloprovincialis* and one in *S. bifurcatus* during autumn. Encysted metacercariae were found scattered during the time of the study and in low numbers; their numbers ranged from 0 to 2 in *M. californianus*, from 0 to 7 in *M. galloprovincialis*, and 0 to 1 in *S. bifurcatus*. Of the three mytilid species, pearls were found most frequently in *M. californianus* and ranged from 0 to 7; in *M. galloprovincialis*, they ranged

from 0 to 5, and from 0 to 1 in *S. bifurcatus*. Larger pearls were found in *M. californianus* where the largest was 2.76 mm in diameter. In *Mytilus galloprovincialis* and *S. bifurcatus*, the largest pearls were 0.92 mm and 0.48 mm, respectively.

In general, *Mytilus californianus* was the most parasitized species when comparing all parasitic loads and pearls in the three mussel species studied (Kruskal-Wallis Test, $H = 1.98$, $P < 0.0001$).

The condition index of mussels studied is shown in Figure 7. One way ANOVA ($F = 4.1$, $P = 0.026$) and Student-Newman-Keuls Method showed that CI was different between *Mytilus californianus* and *Mytilus galloprovincialis*, and also between *M. californianus* and *Septifer bifurcatus*. However, CI was similar between *S. bifurcatus* and *M. galloprovincialis* ($q = 1.34$, ns). Lowest condition indices in *M. californianus* and *M. galloprovincialis* were recorded from autumn to winter when the highest parasite prevalence also occurred and mussels were reproductively active (unpublished data). This pattern was not observed in *S. bifurcatus*.

DISCUSSION

All species from a community are in close relationship, and among them, parasites play an important role in the health status of community members. Living parasite

←

arrow at the right of the worm), the rupture of the gill filaments (arrow at the top), and the clusters of hemocytes around the worm (thin arrow). Scale bar = 50 μ m. Figure 5. Encysted metacercaria in the labial palps of *Mytilus californianus*. The cyst wall is wide and dark. There is no histopathological evidence of host reaction against the cyst. Scale bar = 50 μ m. Figure 6. Trematode cyst in degradation by hemocytes (small arrows) in the *Mytilus galloprovincialis* connective tissue of the digestive gland. Note that the wall of the cyst is broken and clearly distinguishable from the digestive diverticula at the left of the picture. Scale bar = 50 μ m.

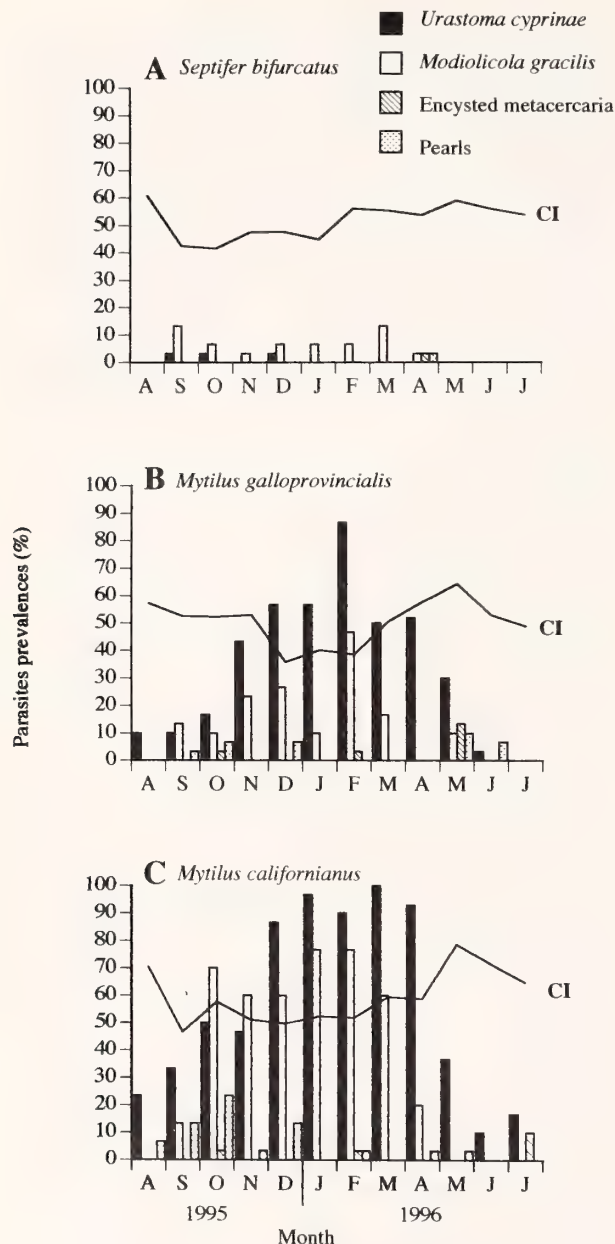


Figure 7

Prevalence of metazoan parasites and pearls in (A) *Septifer bifurcatus*, (B) *Mytilus galloprovincialis*, and (C) *Mytilus californianus* from La Mina del Fraile, an exposed rocky shore in Baja California, Mexico. Lines show the condition index (CI) of mytilids studied.

strategies may be specific for the host species or have multiple species as host (lack of host specificity). This is the case in the present study; all metazoan parasites observed infected all three coexisting mytilids. This suggests that observed parasites have at least three possible hosts. However, parasite prevalence and range for host

species were different. In the first instance, the size of the host seems to be an important factor; the largest mussel, *Mytilus californianus*, was the most infested mytilid, while *Septifer bifurcatus*, the smallest species, was the least infested mussel. In Todos Santos Bay, Ensenada, northwestern Mexico, Cáceres-Martínez et al. (1996) found a significant positive correlation between the size of *Mytilus galloprovincialis* and the presence of the copepod *Pseudomyicola spinosus*; mussels from 45 to 75 mm shell length had the highest number of copepods. In the Black Sea, Murina & Solochenko (1991) found a relationship between the number of the parasitic turbellarian *Urastoma cyprinae* and the size of *M. galloprovincialis*. Mussels from 50 to 70 mm were the most parasitized, while mussels under 30 mm had no parasites. This kind of relationship has also been found for the parasitic copepod *Modiolicola insignis* Aurvillius, 1882, in the Mediterranean Sea by Costanzo & Calafiore (1987). They pointed out that smaller mussels (under 33 mm shell length) were more likely to escape infestation. This observed relationship may be favorable to *S. bifurcatus*, in which the largest size was under 40 mm. Specific studies are needed to determine the reasons for this differential infestation.

The condition index of *Mytilus californianus* and *Mytilus galloprovincialis* was related with their parasitic load and reproductive season during autumn-winter (unpublished data). There was lower CI when highest parasitic loads were recorded and mussels were reproductively active. Histopathological evidence showed that all parasites studied may produce tissue damage. Similar damage in tissues caused by *Urastoma cyprinae* and *Pseudomyicola spinosus* has been described in mussels and oysters (Dinamani & Gordon, 1974; Robledo et al., 1994). The increase in the number of parasites suggests a probable increment in the extension of their associated damages, which in turn could affect the host condition independent of its reproductive stage. High number of parasites related to a low condition index has been shown in a variety of studies (Cole & Savage, 1951; Dare, 1981; Theisen, 1987; Coustau et al., 1990; Murina & Solochenko, 1991; Cáceres-Martínez et al., 1996). The condition index of *S. bifurcatus*, the less parasitized species, was not related to parasitic load, supporting the fact that a low number of parasites may not reflect changes in the CI. However, comparative studies on infected and uninfected mussels at the same reproductive stage must be carried out to determine effect of parasite load on condition of mussels.

In accordance with Stunkard & Uzmann (1958) and Lauckner (1983), the trematode metacercaria cyst recovered from marine bivalves has frequently been misidentified and assigned to various species, mainly of the genus *Himantula*. Encysted metacercaria invade a wide range of bivalve species like *Mytilus edulis* Linnaeus, *Cardium edule* Linnaeus, *Mya arenaria* Linnaeus, and *Macoma baltica* Linnaeus (Lutz, 1980; Lauckner, 1983). Tissue dam-

age observed was similar to that described by Bower (1992). Recorded prevalences are low compared to other studies on encysted metacercaria and mussels (Lutz, 1980). Presence of encysted metacercaria may be connected to the presence of pearls recorded in this study because pearl formation may be induced by encysted trematode infestation (Lutz, 1980; Lauckner, 1983; Bower, 1992). From a pathological point of view, encysted metacercaria resulted in damage to the host, and from a commercial point of view, the presence of pearls in edible mussels (*Mytilus californianus* and *Mytilus galloprovincialis*) may affect consumer acceptance (Lutz, 1980).

If the parasitic load were to affect competitiveness of the host, it is surprising that the most parasitized mytilid species, *M. californianus*, is dominant. This suggests that other factors affect the competitive capacity of *M. galloprovincialis* and *S. bifurcatus*.

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Pea Crab, *Pinnotheres ostreum* Say, 1817, in the Eastern Oyster, *Crassostrea virginica* (Gmelin, 1791): Prevalence and Apparent Adverse Effects on Oyster Gonad Development

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Abstract. Incidence of pea crab, *Pinnotheres ostreum* Say 1817, infestation in the eastern oyster, *Crassostrea virginica* (Gmelin, 1791), was recorded and related to oyster gametogenic activity over 18 months. Sampling occurred at two tidal heights (high intertidal HI and low intertidal LI) at two sites (House Creek, HC and Skidaway River, SR) in Wassaw Sound, Georgia. Overall, incidence rates were 3% HC LI, 1% HC HI, 8% SR LI, and 4% SR HI. At both tidal heights at HC, no differences were observed in gonad area between those oysters with and without pea crabs. At SR (where overall incidences were higher), oysters without pea crabs had significantly higher gonad area values than those oysters with pea crabs present. These results suggest that at higher incidences of pea crab infestation, oyster reproductive capabilities could be impacted, and support the claim that the pea crab/oyster relationship is a parasitic one.

INTRODUCTION

The brachyuran pea crab, *Pinnotheres ostreum* Say, 1817, has been observed in a number of bivalve species, e.g., *Mytilus edulis* Linnaeus, 1758, *Geukensia demissa* (Dillwyn, 1817), *Anomia simplex* d'Orbigny, 1842, and *Pecten* sp. (Williams, 1984). However, it is primarily a parasite (formerly considered a commensal) of the eastern oyster, *Crassostrea virginica* (Gmelin, 1791). This pea crab is found predominantly in the western Atlantic from Massachusetts, United States, to Santa Catarina in Brazil (Williams, 1984). The prevalence of the pea crab in oysters along the eastern seaboard of the United States has generally been high, with prevalences of up to 100% in some subtidal oyster populations in the Chesapeake Bay (Galtsoff, 1964). However, records of pea crab occurrence in the southeastern United States and especially coastal Georgia are scant. Linton (1968) stated that the occurrence of pea crabs in subtidal oysters in coastal Georgia was 100%. However, the vast majority of Georgia oysters occur intertidally (Harris, 1980). Parks (1968) reported that there were substantially higher proportions of pea crabs in oysters found subtidally than in those found intertidally. In the present study, oysters were sampled over a period of 1½ years, and the gonads were examined his-

tologically. Pea crab presence and absence was recorded in the oysters and these data were then related to the gonad condition of the oysters throughout the sampling period.

SITE DESCRIPTION AND METHODS

The two sites chosen for this investigation are shown in Figure 1. House Creek (HC), a shallow sheltered creek, is located on the northern end of Wassaw Sound, Georgia. This site is characterized by relatively high salinities (> 25 ‰) and is sheltered from wave action. The Skidaway River (SR) site, under the Skidaway Institute of Oceanography dock on the north end of Skidaway Island, has more variable salinities and is exposed to higher wave action from passing boats than the House Creek site.

Two tidal heights were chosen for this study. The low-intertidal (LI) area was that area in and around the mean low water mark. The high-intertidal (HI) area was designated as the area above the region designated by the tidal level at approximately 3 hours after mean low water. In coastal Georgia, the majority of oysters occur between these two intertidal boundaries.

Sampling commenced in June 1993 and continued on a biweekly basis until the end of September 1993, when monthly sampling took place. Monthly sampling continued until January 1994. Biweekly sampling recommenced in April 1994 through September 1994.

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Figure 1

Wassaw Sound, Georgia with the two sampling sites indicated: (1) House Creek and (2) Skidaway River near the Skidaway Institute of Oceanography (SkIO).

At each sampling period, 20 ($n = 20$) adult oysters were taken from each tidal height at each site. Upon shucking, the tissue was examined and the presence or absence of pea crabs were recorded. A transverse tissue section (5 mm) was dissected from each shucked oyster and was processed for histological examination and qualitative and quantitative analysis of the gonad tissue according to the methods outlined in O'Beirn et al. (1996). The quantitative parameter used in this study was gonad area which accounted for that proportion, in a standard viewing area of a histological section of the oyster's tissue, occupied by gonad.

Statistical Analysis

Single factor repeated measures analysis was carried out on the data whereby all of the independent variables (oyster height, gonad area) were grouped into two categories—pea crabs present or pea crabs absent. Two dependent variables were examined in the analysis-of-variance (ANOVA): pea crab presence/absence and sampling periods. No interaction term was determined. The variations from the grand mean due to pea crabs and sampling periods will have been accounted for with remaining deviations being the source of error. All proportional data was arcsine square-root transformed prior to analysis. An arbitrary value of ($\alpha = 0.05$) was chosen as the significance level for each ANOVA.

RESULTS

The highest recorded proportion of pea crabs in oysters was at the Skidaway River low intertidal site, where 8%

Table 1

Percent of oysters, *Crassostrea virginica*, according to presence or absence of pea crabs, *Pinnothereus ostreum*. Also given (in parentheses) is the absolute number of oysters in each category.

	PEA CRAB	
	Present	Absent
HOUSE CREEK		
HIGH INTERTIDAL	1% (4)	99% (394)
LOW INTERTIDAL	3% (13)	97% (380)
SKIDAWAY RIVER		
HIGH INTERTIDAL	4% (16)	96% (380)
LOW INTERTIDAL	8% (33)	92% (364)

of oysters sampled throughout the study contained pea crabs (Table 1). The lowest proportion of pea crabs was at the House Creek high intertidal site where 1% of the oysters contained pea crabs (Table 1). Within the sampling periods, the highest incidence of pea crabs in oysters was found in the Skidaway Low Intertidal oysters in April, 1995 where 21% (4 of 19) of the oysters contained pea crabs. No oysters were found containing more than one pea crab.

There were no significant differences in gonad area between those oysters with pea crabs and those without, at both tidal heights at House Creek (HI $P = 0.4152$ and LI $P = 0.8366$; Table 2).

The high intertidal oysters at Skidaway River had significantly higher ($P = 0.0085$) gonad area in oysters without pea crabs, than those with pea crabs (Table 2). The low intertidal oysters also had significantly higher gonad area values ($P = 0.0117$) in oysters where pea crabs were absent than those with pea crabs present (Table 2).

Table 2

Percent gonad area of oysters, *Crassostrea virginica*, according to presence or absence of pea crabs, *Pinnothereus ostreum*. Also given are the p -values of repeated measures analysis using ANOVA.

	PEA CRAB		
	Present	Absent	p -value
HOUSE CREEK			
HIGH INTERTIDAL	38.4%	55.4%	0.4152
LOW INTERTIDAL	54.5%	56.8%	0.8366
SKIDAWAY RIVER			
HIGH INTERTIDAL	38.4%	56.9%	0.0085
LOW INTERTIDAL	42.0%	52.5%	0.0117

DISCUSSION

The number of pea crabs found in oysters in our study is substantially lower than those reported previously for oysters in coastal Georgia. Not surprisingly, in our study, oysters located near the low-tide mark had higher numbers of pea crabs than those located higher in the intertidal zone. A similar phenomenon was reported by Beach (1969) in North Carolina. However, the maximum proportions at any one intertidal height and site of 8% was substantially lower than that of 100% in subtidal oysters as reported previously by Linton (1968). Parks (1968) did record higher instances of pea crabs in subtidal oysters than intertidal oysters. However, the values in Park's (1968) study were in terms of number of pea crabs obtained from a specific number of oysters necessary to give one pint of oyster meat. The number of oysters differed considerably between the sites (tidal heights). Therefore, comparison of Park's (1968) data to those obtained in this study can only be cursory. The disparity between the results of Linton (1968) and this study can be accounted for by the differences in sampling location (subtidal versus intertidal, respectively). However, given that the majority of oysters in coastal Georgia are located intertidally (Harris, 1980), the proportions reported herein are perhaps more reflective of pea crab incidence in oysters in the region.

In Delaware Bay, Flower & McDermott (1952) noted that the proportion of oysters containing pea crabs was higher as they sampled from the upper reaches of the bay toward the ocean, which was concomitant with an increase in salinity. Such a pattern was not observed in this study. In fact, it appears that the higher incidences of pea crabs were found at the Skidaway River site, which traditionally has lower salinities (O'Beirn et al., 1995, 1996; Spruck et al., 1995). The reason for this apparent reversal in prevalence is unclear, but it might be related to the exact location of the House Creek sampling site. All oysters were removed from a small sheltered tidal creek, which is subject to high temperature fluctuations on a daily basis. O'Beirn et al. (1995) reported an 8°C water temperature change at this site in the space of 8 hours in 1991. Also, because of the shallow nature of the creek, it is subject to higher salinity fluctuations caused by freshwater runoff from the marsh, originating from storms which are frequent in the summer months in coastal Georgia. Pea crab development is inhibited by salinities less than 15‰ (Beach, 1969). Assuming the salinities will drop below 15‰, such factors might inhibit free-swimming invasive stages from surviving and hence infesting oysters, at this particular site. A more comprehensive investigation of pea crab incidences along a salinity gradient in the Wassaw Sound, Georgia area would need to be carried out to confirm that our findings were not anomalous. It must be noted that Kruczynski (1974) found no

relationship between presence or absence of pea crabs in *Mytilus edulis* and salinity.

The presence of pea crabs within the mantle cavity of bivalves has been determined to have an adverse effect on the host mollusk. Physical damage to the gills, palps, and gonads of the bivalves has been recorded by a variety of authors (Stauber, 1945; McDermott, 1962; Dix, 1973; Jones, 1977). The presence of pea crabs, *Pinnotheres maculatus* Say, 1818, was deemed responsible for adversely impacting filtration and oxygen consumption rates in *Mytilus edulis* (Bierbaum & Shumway, 1988), as well as having an apparent negative impact on growth rates in nutrient-poor environments (Bierbaum & Ferson, 1986). Tablado & Lopez-Gappa (1995) demonstrated that *Mytilus edulis* individuals harboring mature female pea crabs, *Tumidotheres (Pinnotheres) maculatus* (Say), were significantly smaller and had lower dry weights than those mussels without pea crabs. Bay scallops, *Argopecten irradians concentricus* (Say, 1822), containing adult female pea crabs tended to weigh less and were smaller than those scallops without pea crabs in Bogue Sound, North Carolina (Kruczynski, 1972). Havert (1958) determined that oysters, *Crassostrea virginica*, containing pea crabs, *Pinnotheres ostreum*, had significantly lower dry meat weight and condition indices than oysters without pea crabs. Kruczynski (1972) noted that in the presence of large female pea crabs, the host bivalves tended to have reduced gametogenic output, which was attributed to physical pressure on the gonads.

At both sites in our study, oysters with pea crabs present had lower gonad area values overall than oysters without the pea crabs (Table 2). At the House Creek site, no significant difference in gonad area was determined between those oysters with or without pea crabs. We attribute this to insufficient numbers of infested oysters obtained from this site. The differences at the Skidaway River site were statistically significant, at both tidal heights. In a parallel study (O'Beirn, unpublished studies), oysters in the high intertidal zone tended to have higher quantitative gametogenic parameters than oysters lower down, suggesting that the high intertidal zone was less stressful to the oyster than previously hypothesized (O'Beirn, unpublished studies). In this study, this apparent negative impact of pea crabs on oyster gonad quantity was not confined to these supposedly more stressful environments as was the case with *Mytilus edulis* infested with *Pinnotheres maculatus* (Bierbaum & Ferson, 1986).

The observation in this study that the presence of pea crabs corresponded with lower gonad area measurements in oysters would question the classification of pea crabs as a commensal of oysters. Haines et al. (1994) proposed that the relationship between female pea crabs and their molluscan hosts be classified as true parasitism, as the female is rarely found free-living outside of the host. The results of the findings herein go further to suggest that the pea crabs negatively impact the fitness of oysters. The

significance of these results in terms of pea crab influence on oyster reproduction, must be tempered by the fact that the infestation rates observed were low. Consequently, the impact on the oyster populations in Georgia would appear to be minimal. However, given the high rates of pea crab infestation in oysters reported elsewhere, the apparent negative impact may be extensive and could have more far-reaching implications.

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The Genus *Littoraria* Griffith & Pidgeon, 1834 (Gastropoda: Littorinidae) in the Tropical Eastern Pacific

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Abstract. Six species of *Littoraria* Griffith & Pidgeon, 1834, are recognized in the Panamic Province: *L. pintado pullata* (Carpenter, 1864), *L. varia* (Sowerby, 1832), *L. zebra* (Donovan, 1825), *L. variegata* (Souleyet, in Eydoux & Souleyet, 1852) (= *L. fasciata* of authors, not Gray, 1839), *L. rosewateri* new species, and *L. aberrans* (Philippi, 1846). The shell, reproductive anatomy, and radula of each are described and illustrated. Three possible interspecific hybrids are recorded. *Littoraria pintado pullata* occurs on oceanic rocky shores, but the others are found in mangrove habitats. Distribution maps are given.

This diversity of species is much lower than in the Indo-West Pacific, and only *L. pintado* is common to the two provinces. Morphological comparison does not suggest any obvious sister-species pairs on either side of the Isthmus of Panama, supporting the idea that speciation and/or extinction since the formation of the Isthmus has obscured such relationships. Phylogenetic relationships with other members of the genus are discussed.

Comparisons of shell morphology confirm trends previously demonstrated in Indo-West Pacific species: those species zoned at higher levels on mangrove trees have thinner shells and are more variable (or polymorphic) in shell color. Extreme intraspecific variation in radular morphology is described in three of these species. *Littoraria aberrans* is one of only four ovoviviparous species with intracapsular metamorphosis in the Littorinidae.

INTRODUCTION

The genus *Littoraria* Griffith & Pidgeon, 1834, consists of a group of 36 littorinid species. In cladistic analyses of morphological characters, the genus has been clearly recognized by two unreversed synapomorphies (closed prostate gland and lack of mamilliform penial glands) which, while not individually unique within the family, combine to define it as a monophyletic group (Reid, 1986, 1989). Its members are mainly tropical in distribution and, although some of the basal species occur in the ancestral habitat of the upper eulittoral on rocky shores, the majority show a close and often obligate association with mangroves, wood, and salt-marsh vegetation. In early taxonomic works, species in this group were considered difficult to delimit and characterize, since shells often show interspecific similarities and intraspecific variability, and color polymorphism is common. However, anatomical features, particularly of the reproductive tract, are now known to provide consistent and reliable characters for the identification of *Littoraria* species (Reid, 1986).

Littorinid gastropods are intensively studied because of their abundance, accessibility on the shore, and worldwide occurrence. Within this well-known family, *Littoraria* species show several peculiarities which make them of particular interest. Their association with mangrove and other vegetation is shared by only one other littorinid genus (*Mainwaringia* Nevill, 1885), and aspects of their field ecology, diet, and zonation patterns on the trees have been described (e.g., Reid, 1985; Kohlmeyer & Bebout,

1986; Newell & Bärlocher, 1993; Blanco et al., 1995). Living on trees, often above the regular reach of the tide, they show behavioral and reproductive specializations, including vertical migration (Reid, 1984), lunar spawning rhythms (Berry & Chew, 1973; Gallagher & Reid, 1974), and ovoviviparity (Reid, 1986, 1989). Where sympatric *Littoraria* species occupy different vertical zones on the trees, they provide a clear example of the correlation between the architectural defense of shells and the intensity of crushing by aquatic predators such as crabs and fish (Reid, 1984, 1986, 1992; Cook et al., 1985; Borjesson & Szelistowski, 1989). The species that inhabit the highest levels, among the foliage, often show discrete polymorphism (*sensu* Ford, 1945) of shell color; these provide a model system for the study of maintenance and adaptive significance of color polymorphism (Cook, 1983, 1986, 1990, 1992; Hughes & Mather, 1986; Reid, 1986, 1987; Cook & Garbett, 1992).

The systematics of *Littoraria* are now relatively well understood, particularly in the Indo-West Pacific province, where the 20 mangrove-associated species have been the subject of a taxonomic monograph (Reid, 1986). The remaining species are mostly familiar and easily identified (species lists in Reid, 1986, 1989). The principal clades indicated in a phylogenetic analysis of morphological characters have been recognized as subgenera, although the species-level phylogeny is not well resolved (Reid, 1986, 1989). Nevertheless, those species in the tropical Eastern Pacific have been neglected. Since the earliest faunistic studies of the mollusks in this region

(Adams, 1852; Carpenter, 1857b; Mørch, 1860), the three larger mangrove-associated species have been familiar (generally under the names *L. varia*, *L. fasciata*, and *L. zebra*), although only from their distinctive shells. These have been illustrated in the few modern identification guides for mangrove mollusks from the Panamic province (Zilch, 1954; Keen, 1958, 1971; Peña, 1971b; Alamo & Valdivieso, 1987), but shell characters are variable, and some confusion has persisted. At least in Colombia, they are gathered for food, and are of potential commercial importance (Cantera & Contreras, 1978). A fourth mangrove-associated species, the enigmatic *L. aberrans*, was for over a century known only from the shell of the holotype (Philippi, 1846a), until briefly redescribed by Rosewater (1980b). An additional species, hitherto variously classified as *L. pullata*, *L. pintado*, or *L. pintado schmitti*, occurs on the rocky shores of remote oceanic islands and peninsulas; only the shell has been illustrated (Bartsch & Rehder, 1939; Keen, 1958, 1971; Palmer, 1963; Rosewater, 1970), and its relationship to the Indo-West Pacific *L. pintado* has been considered (Reid, 1986). The anatomy of all these *Littoraria* species of the Eastern Pacific has been examined during the course of recent studies of the phylogeny and classification of the genus (Reid, 1986, 1989), and two electron micrographs of their radulae have been made (Rosewater, 1980a, b). However, no comprehensive descriptions have yet been published. Furthermore, the geographical distributions of these species are not known in any detail.

The present study therefore aims to provide full descriptions of the *Littoraria* species of the tropical Eastern Pacific (Panamic) province. Radular characters are shown to be extraordinarily variable within species. The reproductive anatomy of *L. aberrans* is uniquely modified in the genus, and this is one of only four members of the Littorinidae that are ovoviviparous with intracapsular metamorphosis (Reid & Geller, 1997). One new species, hitherto confused with *L. aberrans*, is described. Nomenclatural revision necessitates a change in the name of *L. fasciata*. The limited ecological information is reviewed, and supplemented by field observations. Distribution maps are plotted for each species, and their biogeography and relationships discussed in the context of the geological history of Central America.

MATERIALS AND METHODS

This account is based on examination of all material in the collections of the Natural History Museum, London (BMNH), the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM), the Academy of Natural Sciences of Philadelphia (ANSP), and the Museum of Comparative Zoology, Harvard University (MCZ). Personal collections of all species were made in Costa Rica (1985) and Mexico (1994), and are deposited in BMNH. Additional material was borrowed

from the Los Angeles County Museum of Natural History (LACM) and the California Academy of Sciences (CAS). All available type material was examined.

Shell dimensions were measured with vernier calipers to 0.1 mm. Shell height (H) is the maximum dimension parallel to the axis of coiling, shell breadth (B) the maximum dimension perpendicular to H, and the length of the aperture (LA) the greatest length from the junction of the outer lip with the penultimate whorl to the anterior lip. For the purpose of diagnosis, shell shape was quantified simply as the ratio H/B and H/LA (relative spire height, SH), and the range of these ratios quoted. Protoconch whorls were counted as recommended by Reid (1996). To describe the coiling of the operculum, the opercular ratio was defined as the ratio of two parallel measurements, the diameter of the spiral part divided by the maximum length (Reid, 1996). The relative radular length was the total radular length divided by shell height.

Living animals were relaxed in 7.5% (volume of hydrated crystals to volume of fresh water) magnesium chloride solution. Sperm samples were removed from the seminal vesicles of relaxed, living animals, fixed in 0.5% seawater formalin, examined immediately by light microscopy, and drawn by camera lucida. Animals were fixed in 10% seawater formalin buffered with borax, and stored in 80% ethanol before dissection. For general accounts of the male and female anatomy of *Littoraria*, see Reid (1986). Radulae were cleaned by soaking in a hypochlorite bleaching solution at room temperature for about 5 min, rinsed in distilled water, mounted on a film of polyvinyl acetate glue on glass, allowed to dry in air, and coated with gold and palladium before examination in a scanning electron microscope. Unworn portions of radulae were viewed in three orientations: in standard flat view from vertically above the radula (to show shapes of teeth), at an angle of 45° from the front end of the radula (to show shapes of tooth cusps), and at an angle of 45° from the side of the radula (to show relief). The shape of the rachidian tooth was quantified as the ratio of the total length (in flat view) to the maximum basal width. The "hood" of the rachidian is a sharp flange (presumably an additional cutting edge) anterior to the main cusps of the tooth.

The supraspecific classification employed follows that of Reid (1989).

SYSTEMATIC DESCRIPTIONS

Family LITTORINIDAE Anon., 1834

Genus *Littoraria* Griffith & Pidgeon, 1834

Type species: *Littorina pulchra* "Gray" Sowerby, 1832 [= *Turbo zebra* Donovan, 1825]

Diagnosis: Littorinidae without nodulose shell sculpture, with paucispiral operculum, egg groove of pallial oviduct coiled in a single spiral, salivary glands constricted by nerve ring; defining (but not unique) synapomorphies are

closed prostate gland and absence of mamilliform penial glands (after Reid, 1989).

Subgenus *Protolittoraria* Reid, 1989

Type species: *Turbo pintado* Wood, 1828

Diagnosis: Penis not bifurcate; scattered simple penial glands not forming discrete glandular disc; copulatory bursa opening at posterior end of straight section of pallial oviduct; spawn of cupola capsules sculptured by one concentric ring; hood of rachidian tooth slight or absent; six to eight elongate cusps on outer marginal tooth (diagnosis modified from Reid, 1989).

Littoraria (Protolittoraria) pintado pullata (Carpenter, 1864)

(Figures 1, 2A–C, 3A, 4A, B, 5A–E, 6A)

- Littorina* sp. Carpenter, 1857b: 350 (see Carpenter, 1864a).
Littorina pullata Carpenter, 1864a: 477 (Cape St Lucas [Cape San Lucas, Baja California, Mexico]; lectotype (here designated, 11.3 mm, Figure 1B) USNM 12661, seen; 2 paralectotypes USNM 635481, seen; 7 paralectotypes BMNH 1865.12.6.69, seen; 3 paralectotypes BMNH 1968357, seen; 3 paralectotypes ANSP 18627, seen). Carpenter, 1864b: 546, 618. Weinkauff, 1882: 106.
Littorina (Melaraphe) pullata—Keep & Baily, 1935: 199.
Littorina (Melaraphe) scutulata pullata—Burch, 1945: 12. Palmer, 1958: 159.
Littorina pullata—Keen, 1958: 282; fig. 177. Palmer, 1963: 335–336; pl. 61, fig. 6. Keen, 1971: 366; fig. 186. Abbott, 1974: 69.
Littorina (Littoraria) pullata—Rosewater, 1970: 423, 447.
Littoraria pintado pullata—Reid, 1996: 11.
Littorina (Melaraphe) scutulata—Tryon, 1887: 250; pl. 45, fig. 3 (in part, includes *Littorina scutulata* and *Littorina plena*; not Gould, 1849).
Littorina scutulata—Abbott, 1974: 67–68 (in part, includes *Littorina scutulata* and *Littorina plena*; not Gould, 1849).
Littorina schmitti Bartsch & Rehder, 1939: 9–10; pl. 2, fig. 4 (shore south of landing, Clipperton Island; holotype USNM 472547, Figure 1F, seen). Keen, 1971: 366; fig. 187.
Littorina (Littoraria) pintado schmitti—Rosewater, 1970: 423, 449–450; pl. 346, figs 13–16.
Littoraria (Littoraria) pintado—Reid, 1986: 64, 73 (not *Turbo pintado* Wood, 1828, which is the nominate subspecies).
Littoraria (Protolittoraria) pintado—Reid, 1989: 96 (not Wood, 1828).

Taxonomic history: Despite an adequate initial description (Carpenter, 1864a), this subspecies has long remained misunderstood and poorly known. Following Tryon (1887), it has often been considered a color form or subspecies of *Littorina scutulata* (Burch, 1945; Palmer, 1958; Abbott, 1974; see Reid, 1996). Bartsch & Rehder (1939) gave the name *Littorina schmitti* to examples from Clipperton Island, and noted a relationship to "*Littorina*"

pintado from the Indo-West Pacific. However, the conspecificity of Mexican specimens with those from Clipperton Island, and with *Littoraria pintado*, was only pointed out much later (Reid, 1986).

Diagnosis: Shell smooth with fine incised spiral lines, brown to black, often with pale flecks and spiral lines, aperture brown, columellar pillar white. Penis long, simple, no glandular structures visible externally.

Shell (Figure 1): Mature shell height 5–16.9 mm. Shape high-turbinate to elongate ($H/B = 1.47$ – 1.71 , $SH = 1.47$ – 2.02); spire whorls only slightly rounded, sutures slightly impressed; indistinct angulation at periphery of last whorl; of moderate thickness. Mature lip not flared; columellar pillar long, straight and somewhat flattened, only slightly hollowed at base. Sculpture smooth except for fine incised spiral lines over whole surface, 8–13 above periphery of last whorl, but often indistinct or obsolete; entire surface with fine spiral microstriae if well preserved; no discernible periostracum. Protoconch 0.30 mm diameter, about 3.5 whorls, terminated by sinusigera rib, sculpture not preserved. Color: densely pigmented, largely obscuring pale ground color; effect is chocolate brown to black with variable patterning of pale grey to white: finely flecked, marbled or tessellated, alternatively with narrow spiral lines (2–17 on last whorl), or combination of flecks and lines; pale patterning usually stronger on base and from shoulder to suture; shell rarely almost entirely black. Columellar pillar white, edged with chocolate brown; interior blackish brown with pale lines showing through.

Animal: Head, tentacles, and sides of foot dark grey to black, sometimes a pale stripe behind eye and pale spot at inside of tentacle base. Opercular ratio 0.31–0.36. Penis (Figure 2A–C) long, vermiform, tapering only near tip; fine annular wrinkles extend almost to tip, so that filament is not differentiated from base; base not bifurcate, no glandular disc visible externally, but base probably contains simple subepithelial glandular cells (as confirmed by histological examination of nominate subspecies, Reid, 1989); sperm groove open (also anterior vas deferens from prostate), extending to tip of filament; unpigmented except for small grey or blackish area at very base. Euspermatozoa 107–114 μm ; paraspermatozoa (Figure 3A) spherical to oval, maximum diameter 15–22 μm , packed with large spherical granules (to 6 μm diameter), single rod-pieces small and often irregular (6–14 μm long). Pallial oviduct (Figure 4A, B) with spiral section of 3.5 whorls, of which capsule gland (with proximal opaque and distal translucent portion) about two-thirds of a whorl; bursa small, at posterior end of straight section of pallial oviduct. Spawn and development not observed; presence of capsule gland suggests pelagic egg capsule (pelagic cupola capsule with single annular ridge and single ovum described in nominate subspecies;

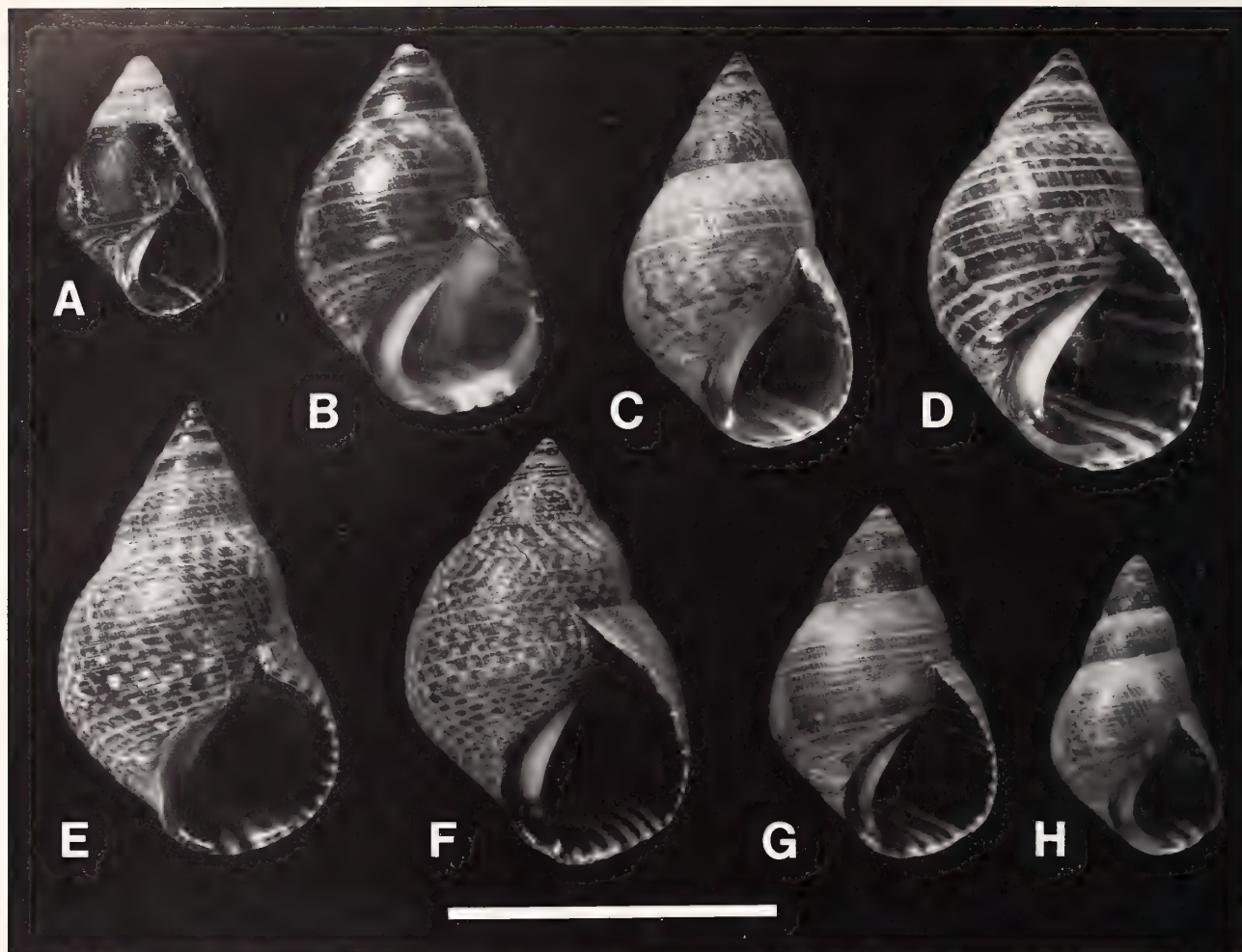


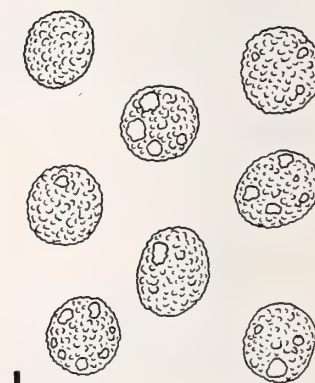
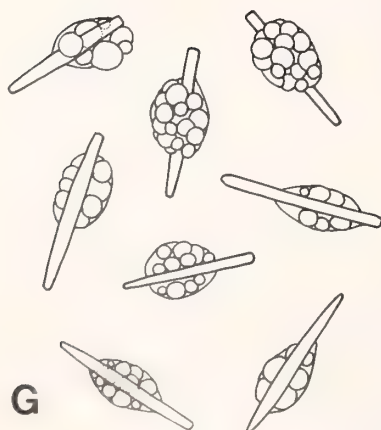
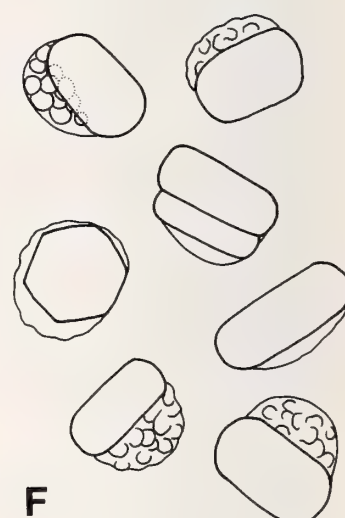
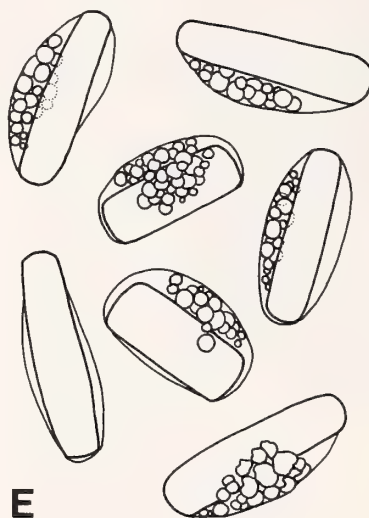
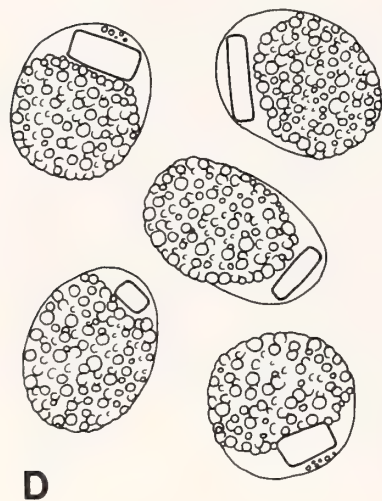
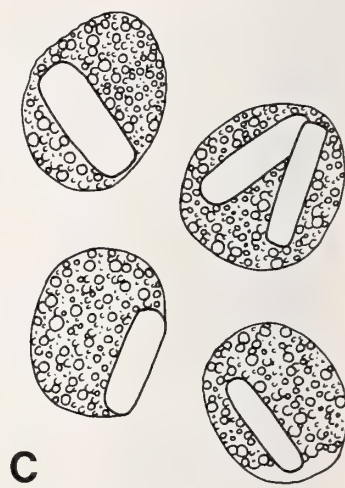
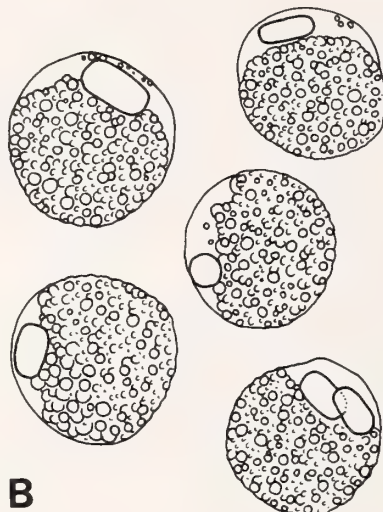
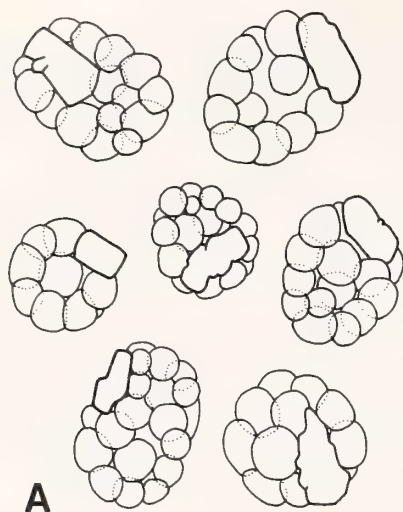
Figure 1

Shells of *Littoraria pintado pullata*. A. Bahía Santa María, Baja California, Mexico (BMNH 1996198; small, black shell form from algal pools at top of eulittoral zone). B. Lectotype of *Littorina pullata* Carpenter, 1864 (USNM 12661); Cabo San Lucas, Baja California, Mexico. C. Socorro Island, Mexico (CAS 96233). D. Cabo San Lucas, Baja California, Mexico (BMNH 1996199). E. Punta Arena, Cerralvo Island, Gulf of California, Mexico (CAS 107727). F. Holotype of *Littorina schmitti* Bartsch & Rehder, 1939 (USNM 472547); Clipperton Island. G. Cabo San Lucas, Baja California, Mexico (BMNH 1996199). H. María Madre Island, Tres Marias Islands, Mexico (CAS 32564). Scale bar = 10 mm.

Figure 2

Penes and heads of *Littoraria pintado pullata* (A–C), *L. variegata* (D, E, L), *L. varia* (F, G, J, K) and *L. zebra* (H, I). A–C. Penes of *L. pintado pullata*. A, B. Cabo San Lucas, Baja California, Mexico (BMNH 1996209; shell H of A = 9.7 mm, shell H of B = 10.4 mm). C. Bahía Santa María, Baja California, Mexico (BMNH 1996210; shell H = 7.1 mm). D, E. Penes of *L. variegata*. D. Punta Morales, Golfo de Nicoya, Costa Rica (BMNH 1996211; shell H = 20.3 mm). E. Topolobampo, Sinaloa, Mexico (BMNH 1996212; shell H = 15.9 mm). F, G. Penes of *L. varia*. F. Punta Morales, Golfo de Nicoya, Costa Rica (BMNH 1996213; shell H = 19.5 mm). G. Panama (BMNH 1867.5.22.27; shell H = 28.9 mm). H, I. Penes of *L. zebra*. H. Golfito, Costa Rica (BMNH 1996214; shell H = 26.8 mm). I. Puntarenas, Costa Rica (BMNH 1996215; shell H = 29.8 mm). J. Penis of *L. varia*; Punta Morales, Golfo de Nicoya, Costa Rica (BMNH 1996213; shell H = 19.1 mm). K. Head of *L. varia*; Punta Morales, Golfo de Nicoya, Costa Rica (BMNH 1996213). L. Head of *L. variegata*; Topolobampo, Sinaloa, Mexico (BMNH 1996212). Abbreviations: f, penial filament; pd, penial glandular disc.





20 μ m

Struhsaker, 1966); type of protoconch indicates planktonic development.

Radula (Figure 5A–E): Relative radular length 1.46–4.09. Rachidian: length/width 0.92–1.37; cusps variable: central cusp pointed (Figure 5D), elongate leaf-shaped (Figure 5E) or very elongate with rounded tip (Figure 5B); smaller pointed cusp and outer denticle on either side; hood developed only as small ridge (Figure 5C–E), or sometimes absent (Figure 5A, B). Lateral: five to six cusps, largest central cusp elongate, but variable in shape (pointed, leaf-shaped or bluntly rounded); two small pointed cusps on inside and two to three on outside of main cusp. Inner marginal: four cusps, largest central cusp shaped like that on lateral; two smaller pointed cusps on inside and one on outside of main cusp. Outer marginal: six to eight elongate pointed cusps, outermost largest. See Remarks.

Material examined: Types as indicated; 26 lots; two protoconchs; nine penes; two sperm samples; six pallial oviducts; eight radulae. (Of nominate subspecies: lectotype of *Turbo pintado* Wood, 1828, BMNH 1968368; 50 lots; one protoconch; seven penes; three sperm samples; four pallial oviducts; three radulae).

Habitat: On rock (including granite, beachrock, and concrete) in uppermost eulittoral and low littoral fringe, clustered in crevices and on sides of rocks; at one locality (Bahía Santa María, NE of Cabo San Lucas, Baja California) submerged or clustered at margins of small algal pools at top of shore; usually on strongly wave-exposed shores. Occurs only at sites with clear, oceanic water. Abundant only at tip of Baja California and on oceanic islands (e.g., 5375 per m² at Socorro Island (Mille-Pagaza et al., 1994).

Range (Figure 6A): Southern Baja California from Todos Santos (BMNH) to 35 km N of La Paz (24°21'N; BMNH; but common only close to Cabo San Lucas); Clarion Island and Socorro Island in the Revillagigedo Islands (CAS, LACM); Tres Marias Islands (CAS); Clipperton Island (USNM). There is also a single collection of four specimens from Cocos Island (5°33'N, LACM) much farther to the southeast; since this species is characteristically found on oceanic islands, this record is

probably reliable. Only occasional specimens have been found on the mainland of Mexico, e.g., 25 km SW Puerto Vallarta (BMNH), 10 km N of Melaque (18°48'N; BMNH), and recorded from Mazatlán (Carpenter, 1857b, 1864a). Records from the state of California (e.g., Burch, 1945; Abbott, 1974) are believed to be misidentifications of *Littorina scutulata* and/or *Littorina plena* Gould, 1849, as in one lot in CAS.

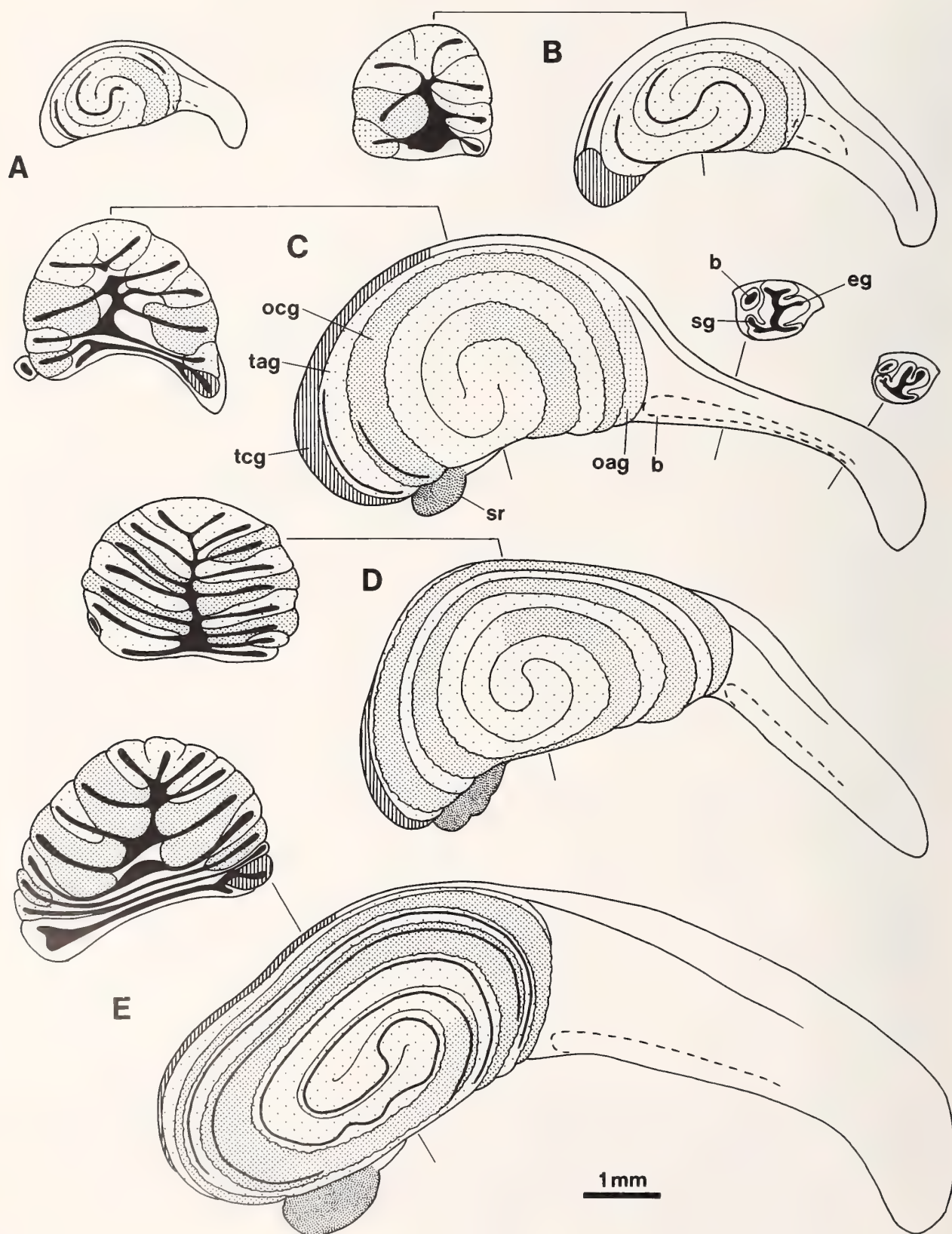
Remarks: The nominate subspecies, *L. pintado pintado*, has a very wide distribution in the Indo-West Pacific; this range is disjunct, with one area in the south and western Indian Ocean (southeast Africa, Madagascar, Mascarene Islands, Somalia) and another in the northern and western Pacific (Ryukyu, Bonin, Caroline, Mariana, Marshall, and Hawaiian Islands) (Rosewater, 1970; Reid, 1986). Although the two areas of occurrence are separated by about 8000 km, no consistent morphological differences in shells, anatomy, or radulae have been detected (personal observation).

The Eastern Pacific records of *L. pintado pullata* are at least 4500 km from the closest known occurrence of the nominate subspecies in the Indo-West Pacific, in the Hawaiian Islands. The close relationship between Eastern Pacific and Indo-West Pacific forms was first noted by Bartsch & Rehder (1939) when they described shells from Clipperton Islands as a new species, *schmitti*, although they did not mention *pullata*. Curiously, Rosewater (1970) reduced *schmitti* to a subspecies of *pintado*, while remarking that *pullata* was an “apparent analogue” of *pintado* in the Eastern Pacific. Reid (1986) found no differences in the reproductive anatomy of *pullata* and *pintado*, and synonymized all three names. This has been confirmed in the present study of additional material, which has included examination of sperm and radulae. However, there are consistent differences in shell coloration. Since all known species of *Littoraria* differ from each other in penial shape (Reid, 1986), separation at specific level does not seem warranted at present. The category of subspecies is appropriate for such a case of minor differentiation combined with allopatric distribution, and carries the implication that although the differentiation probably reflects genetic isolation, there is no morphological evidence for reproductive isolation. In the

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Figure 3

Paraspermatozoa of *Littoraria pintado pullata* (A), *L. varia* (B, C), *L. zebra* (D), *L. variegata* (E, F), *L. rosewateri* Reid, sp. nov. (G, H) and *L. aberrans* (I). A. Cabo San Lucas, Baja California, Mexico (BMNH 1996209). B. Punta Morales, Golfo de Nicoya, Costa Rica (BMNH 1996213). C. Estero Aguadulce, Bahía Parita, Panama (USNM 733057; alcohol preserved). D. Punta Morales, Golfo de Nicoya, Costa Rica (BMNH 1996216). E. Punta Morales, Golfo de Nicoya, Costa Rica (BMNH 1996211). F. Estero Aguadulce, Bahía Parita, Panama (USNM 733055; alcohol preserved, therefore granules indistinct). G, H. Golfito, Costa Rica (BMNH 1996217). I. Punta Morales, Golfo de Nicoya, Costa Rica (BMNH 1996218). All samples from single individuals; unless otherwise noted, all samples fixed in 0.5% seawater formalin.



nominate subspecies, coloration is predominantly white to pale grey, with spiral rows of small black or brown spots or flecks (18–40 rows on final whorl); although the spotting may occasionally be quite dense, the spots do not fuse to form spiral bands. In contrast, in *L. pintado pullata* the predominant coloration is black to brown, and in addition to varying degrees of pale spotting or marbling, most specimens show white spiral lines.

The geographical distribution of *L. pintado* is of particular interest, since it is one of the few molluscan species, and the only littorinid, to span both Indo-West Pacific and Eastern Pacific provinces. These zoogeographic regions are separated by "Ekman's Barrier," a 5000 km expanse of deep ocean without island stepping stones, which appears to have acted as an effective barrier for most shallow-water benthic invertebrates (Vermeij, 1987; Richmond, 1990). However, the barrier is not complete; although almost no Panamic mollusks are known from the Indo-West Pacific, a small number of typically Indo-West Pacific species have been recorded in the Eastern Pacific. The most recent compilation of these listed 61 prosobranch gastropods, of which 56% are found only on the oceanic islands off the American mainland (Emerson, 1991). The rarity of most of these species, combined with their absence from the limited fossil record of western Central America, suggests that the majority are recent (post-Pliocene) arrivals derived by dispersal from the Central Pacific, and that many of the species may be unable to maintain viable populations without replenishment from the source areas to the west (Emerson, 1991). Eastward dispersal is believed to take place mainly by larval transport in the North Equatorial Countercurrent, in which drifter buoys have covered the distance from the Line Islands to the Eastern Pacific in as little as 100 days (Richmond, 1990). Most of the Indo-West Pacific immigrants, particularly the tonnoideans, are known to possess long-lived (teleplanic) larvae able to survive in the plankton for this length of time (Scheltema, 1988). During the periodic El Niño events which considerably alter oceanographic patterns in the Central and Eastern Pacific, this passage may be accomplished in half the time, but the main source area is still considered to be in the Line Islands, lying in the eastward flow of the North Equatorial

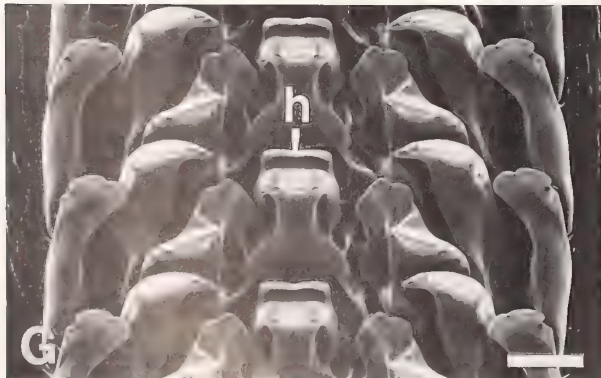
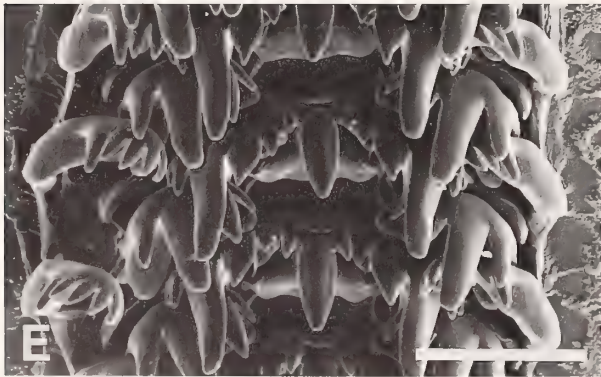
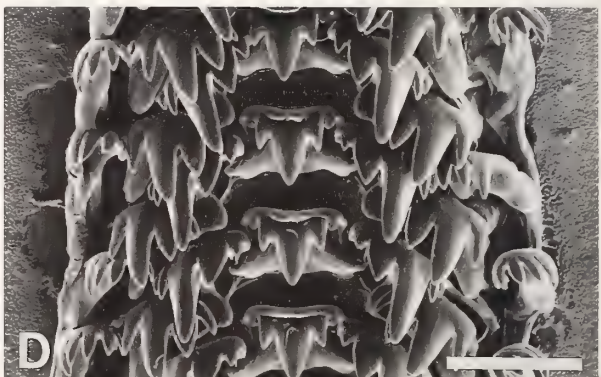
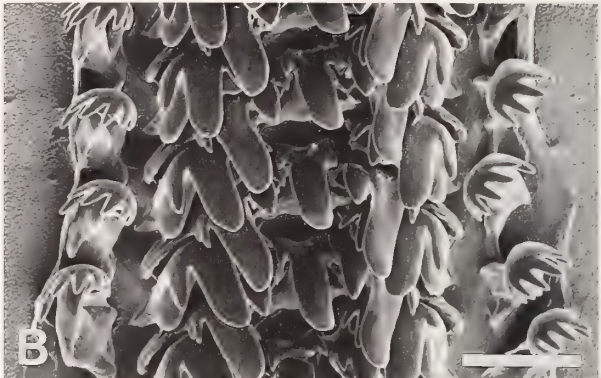
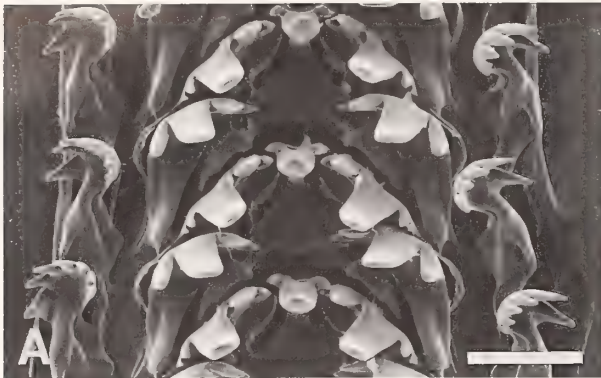
Countercurrent (Richmond, 1990). The evolutionary consequences of trans-Pacific dispersal appear to have been limited. For ecological reasons, some arrivals in the Eastern Pacific may be unable to maintain viable populations there. In those that do, trans-Pacific dispersal is apparently frequent enough to prevent isolation and genetic divergence in the Eastern Pacific; among gastropods, only four Eastern Pacific species or subspecies (excluding *L. pintado pullata*) were interpreted as endemic derivatives of recent immigrants from the Indo-West Pacific by Vermeij (1990).

In many respects, however, *L. pintado* does not conform to the distributional and developmental characteristics shown by other gastropods with trans-Pacific distributions. Quite clearly, *L. pintado pullata* maintains viable populations in the Eastern Pacific, at least in Baja California and on the oceanic islands where it is abundant. Indeed, throughout the range of the species as a whole, it seems to be found largely on oceanic islands, and this habitat specialization explains its almost complete absence from the mainland of Mexico and Central America. Whether the island populations are in genetic contact is unknown, but surface current patterns (Wyrski, 1965) suggest that this is possible. During the period May to December, the strong North Equatorial Countercurrent could perhaps transport egg capsules and larvae from Clipperton Island to Cocos Island to the east, sweeping northwestward parallel with the Mexican coast toward the Revillagigedo Islands. During the winter this current disappears, while from February to June the California Current flows south and southeast, turning westward to join the North Equatorial Current, thus potentially connecting the populations of Baja California, the Revillagigedo Islands, and Clipperton Island. The spawning season in the Eastern Pacific is unknown, but in Hawaii *L. pintado pintado* produces egg capsules all year round (Struhsaker, 1966). The length of larval life has not been recorded; when reared in the laboratory in Hawaii, veligers survived for 11 days from the time of spawning (Struhsaker, 1966). In a littorinid species with a similar protoconch, *Nodilittorina hawaiiensis* Rosewater & Kadolsky, 1981, the total time to larval settlement in the laboratory was 3–4 weeks (Struhsaker & Costlow, 1968, as *Littorina pic-*

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Figure 4

Pallial oviducts of *Littoraria pintado pullata* (A, B), *L. varia* (C), *L. variegata* (D) and *L. zebra* (E). A. Bahía Santa María, Baja California, Mexico (BMNH 1996210; shell H = 8.8 mm). B. Cabo San Lucas, Baja California, Mexico (BMNH 1996209; shell H = 12.6 mm). C. Punta Morales, Golfo de Nicoya, Costa Rica (BMNH 1996213; shell H = 25.2 mm). D. Punta Morales, Golfo de Nicoya, Costa Rica (BMNH 1996211; shell H = 22.0 mm). E. Golfoito, Costa Rica (BMNH 1996214; shell H = 27.0 mm). Transverse sections taken at levels indicated, viewed from anterior (i.e., right side of figure). Abbreviations: b, copulatory bursa (dashed line; visible only by dissection); eg, egg groove (visible externally if darkly pigmented, as in E, then indicated by thick line); oag, opaque albumen gland (light stipple); ocg, opaque capsule gland (dark stipple); sg, sperm groove (leading ventrally to seminal receptacle); sr, seminal receptacle (darkest stipple); tag, translucent albumen gland (lightest stipple); tcg, translucent capsule gland (cross-hatched); in sections, spiral lumen is black.



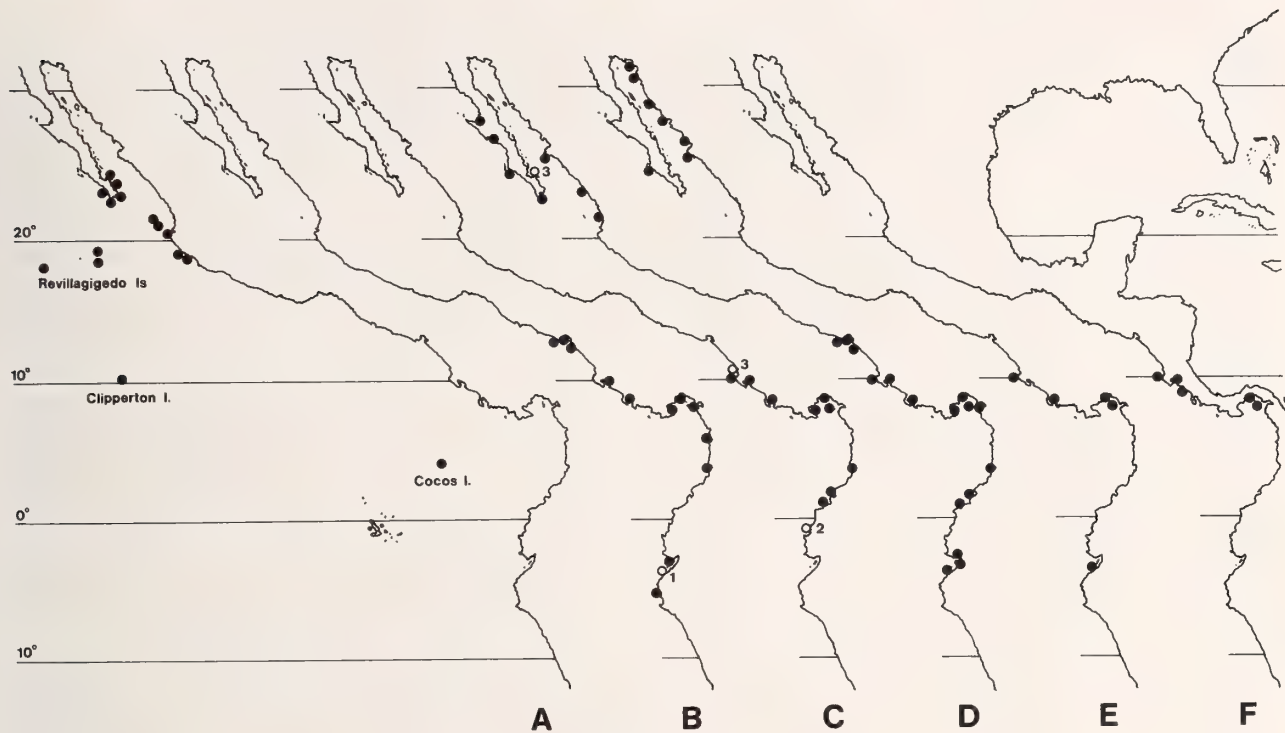


Figure 6

Distribution maps of six Eastern Pacific *Littoraria* species. A. *L. pintado pullata*. B. *L. varia*. C. *L. zebra*. D. *L. variegata*. E. *L. rosewateri* Reid, sp. nov. F. *L. aberrans*. Key: closed circles, material examined; open circles, records from literature (1, Peña, 1970, 1971b; 2, Guerrini, 1990; 3, Pilsbry & Lowe, 1932).

ta). This is sufficient to permit transport for approximately 1000 km at some of the faster average current flows suggested by Wyrki (1965), but is much shorter than the developmental times of long-lived teleplanic larvae (Scheltema, 1988). Larval dispersal between the more distant islands is therefore unlikely to be frequent in normal seasons, but might take place under the exceptional conditions of El Niño events (Richmond, 1990). *Littoraria pintado pullata* is notably absent from the Galápagos Islands (Finet, 1994) which, although only 750 km from Cocos Island, lie outside the path of the North Equatorial Countercurrent (Finet, 1991). Another peculiarity of *L. pintado* in this context is that it is distributed in the

northern Central Pacific (Rosewater, 1970; personal observation of museum collections), the closest occurrence to the Eastern Pacific being in the Hawaiian Islands. In comparison, all but one of the other 60 trans-Pacific prosobranchs listed by Emerson (1991) occur in the Line Islands and/or French Polynesia (although many do in addition occur in the Hawaiian Islands). Since the Hawaiian Islands are so distant (about 4500 km) from the range of *L. pintado pullata*, and furthermore lie in the weak westward-flowing North Equatorial Current (McNally et al., 1983), it is improbable that there is any gene flow between the populations in the Indo-West Pacific and the Eastern Pacific, even during the exceptional El Niño

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Figure 5

Radulae of *Littoraria pintado pullata* (A–E) and *L. variegata* (F–H). A, B. Cabo San Lucas, Baja California, Mexico (BMNH 1996209; two views of radula, flat and at 45°; shell H = 10.4 mm). C, D. Bahía Santa María, Baja California, Mexico (BMNH 1996210; two views of radula, flat and at 45°; shell H = 8.8 mm; small, black shell form from algal pools at top of eulittoral zone). E. Bahía Santa María, Baja California, Mexico (BMNH 1996210; at 45°; shell H = 8.7 mm; normal shell form from open rock surfaces). F. Topolobampo, Sinaloa, Mexico (BMNH 1996212; at 45°; shell H = 15.9 mm). G, H. Punta Morales, Golfo de Nicoya, Costa Rica (BMNH 1996211; two views of radula, flat and at 45°; shell H = 20.3 mm). Abbreviation: h, “hood” of rachidian tooth. Scale bars = 50 µm.

events (Richmond, 1990). This likely genetic isolation may be reflected by the consistent differences in the shell pigmentation of the two, and these arguments support the assertion that *L. pintado pullata* should be recognized at least as a distinct subspecies. Information on the genetic interrelationships of *L. pintado* throughout its range would be most desirable.

Unfortunately, littorinids of high-energy rocky shores are seldom preserved as fossils, and the marine Tertiary record of western Central America is poor, so that there is no fossil evidence for the history of *L. pintado* in the Eastern Pacific. Nevertheless, the evidence reviewed above does suggest that *L. pintado* is not in the same category as those other non-tonnoidean gastropods with trans-Pacific distributions, which have been interpreted as recent colonizers, sometimes tenuously established, which have in general not differentiated from their parent populations in the Central Pacific (Vermeij, 1987, 1990; Emerson, 1991). Instead, *L. pintado pullata* can be added to the four possible examples of Eastern Pacific endemic gastropods derived from Indo-West Pacific immigrants (listed by Vermeij, 1990). The origin of *L. pintado pullata* is still likely to have been relatively recent in geological terms, since the islands on which it occurs are all of Pleistocene age, and elsewhere in the Eastern Pacific only the Galápagos are older (Emerson, 1978). Although dispersal from the Hawaiian Islands to the Eastern Pacific appears to be unlikely under present conditions, *L. pintado* may have been more widely distributed in the Central Pacific in the past. For example, during the sea level fluctuations of the Pleistocene, suitable habitat (high oceanic islands lacking well-developed reefs) may have been more widespread. An alternative scenario, not requiring dispersal across the Pacific, is that the distribution of *L. pintado* is an ancient one, predating the Miocene division of the Tethys Sea and the Pliocene formation of the Isthmus of Panama. This is not credible, in view of the geological ages of the Eastern Pacific islands. Furthermore, the morphological identity of the two subspecies is unlikely to have been maintained if they have been separated since vicariance of an ancient Tethyan distribution. Once again, genetic evidence will be valuable in testing this assertion.

Morphologically, this species is of interest as it shows a number of features suggesting that it is the basal branch within the clade *Littoraria* (phylogenetic analyses by Reid, 1986, 1989). These include the cupola-type egg capsule (biconvex elsewhere in the genus), lack of a discrete penial glandular disc, and the poorly developed or absent hood on the rachidian radular tooth (hitherto recorded only as absent; Reid, 1986, 1989). If correct, this implies that *L. pintado* (or the clade of which it is the only surviving member) is at least as old as any other *Littoraria* species. Other members of this genus are recorded from the Lower Eocene (Reid, 1989). This does not, however, affect the biogeographic scenarios dis-

cussed above, which depend upon the age of the separation of the two subspecies, and not on that of the clade.

Radular variation is striking in this species. Five specimens from Bahía Santa María, Baja California, suggest a possible correlation with shell form or habitat. Two examples of a peculiar small (< 8.8 mm) almost black shell form, with eroded spire, collected from the unusual habitat of algal pools high on the shore (Figure 1A), showed radulae with relatively smaller and more pointed major cusps, and more well developed rachidian hood (Figure 5C, D). Three shells of typical form (7.2–14.7 mm), collected on open rock surfaces at the same locality (similar to Figure 1D), showed radulae with more elongate cusps and only slightly hooded rachidian (Figure 5E); these were similar to examples from Cabo San Lucas (Figure 5A, B), and to specimens of *L. pintado pintado* from Hawaii and Mauritius. No other anatomical differences were detected among specimens from Bahía Santa María. Further investigation is required, but a possible explanation of these preliminary observations is an ecophenotypic effect on radular tooth shape, as has recently been demonstrated in the littorinid *Lacuna* (Padilla, 1998).

This species is common only near Cabo San Lucas and on the relatively inaccessible offshore islands, which explains why it has remained poorly known, and has seldom been figured or described. Among other littorinids in the Panamic province, confusion is possible with *Nodilittorina* species such as *N. aspera* (Philippi, 1846) and *N. penicillata* (Carpenter, 1864); these shells are separated by their entirely brown columella and more pronounced oblique axial stripes of black and white; anatomically, *Nodilittorina* species have a bifurcate penis with a glandular disc and single mamilliform gland, and a pallial oviduct with single loop in the albumen gland only (Reid, 1989). In the Californian province, *Littorina scutulata* and *Littorina plena* are similar in shell outline, but generally show coarser tessellation and lack spiral lines except on the base; their penes have glandular protrusions and there are three consecutive spiral loops in the pallial oviduct (Reid, 1996). The distinction from the nominate subspecies in the Indo-West Pacific has been described earlier.

Subgenus *Littoraria* Griffith & Pidgeon, 1834

Diagnosis: Penis usually bifurcate, with differentiated penial glandular disc; paraspermatozoa lacking pseudotrich (Healy & Jamieson, 1993; "flagellum" of Reid, 1986, 1989); spawn of biconvex discoidal capsules; rachidian tooth usually hooded (diagnosis modified from Reid, 1989). Note that phylogenetic analysis of Reid (1989) suggested this is a paraphyletic or polyphyletic assemblage.

Littoraria (*Littoraria*) *varia* (G.B. Sowerby, 1832) (Figures 2F, G, J, K, 3B, C, 4C, 6B, 7A–C, 8A–E)

Littorina varia G.B. Sowerby, 1832: part 37; pl. 211, fig. 4
(Panama; lectotype (here designated) Sowerby, 1832:

- pl. 211, fig. 4). Adams, 1852: 400–401. Souleyet, in Eydoux & Souleyet, 1852: 561; atlas pl. 31, figs 43–45 (as “*Littorina costulée*” in caption). Reeve, 1857: *Littorina* sp. 19; pl. 4, fig. 19a, b. Mörch, 1860: 69. Dall, 1909: 231, 285 (in part, includes *Littoraria variegata*). Keen, 1958: 282; fig. 178. Keen, 1971: 366; fig. 188. Peña, 1971b: 47. Rosewater, 1980a: 5; figs 3, 4 (radula). Guerrini, 1990: 14.
- Littorina varia*—Philippi, 1846b: 2: 99–100; *Littorina* pl. 1, figs 2, 3. Weinkauff, 1882: 53; pl. 6, figs 14, 15.
- Littorina (Melaraphe) varia*—Tryon, 1887: 246; pl. 43, fig. 44 (in part, includes *Littoraria variegata*).
- Littorina (Littorinopsis) varia*—von Martens, 1900: 580. Rosewater, 1970: 423. Alamo & Valdivieso, 1987: 25; fig. 38.
- Littorina (Algaroda) varia*—Zilch, 1954: 81; pl. 3, fig. 8.
- Littoraria (Littoraria) varia*—Reid, 1986: 73; figs 4j (penis), 18 (cladogram). Reid, 1989: 97.
- ?*Littorina perdix* King & Broderip, 1832: 345 (no locality; types lost).
- Littorina costulata* ‘Souleyet’ Tryon, 1887: 246, 292 (*nomen nudum*).
- Littorina (Littorinopsis) fasciata*—Abbott, 1974: 69; pl. 3, fig. 567 (in part; includes *Littoraria variegata*; not Gray, 1839 = *Littoraria zebra*).

Taxonomic history: No type specimens are known to exist and a lectotype figure is here designated. Nevertheless, there is no uncertainty about the identity of this taxon, and the name *varia* has been employed by most authors, in various generic combinations, throughout its history. Tryon (1887) and Dall (1909) had a broader concept of this taxon, including *L. variegata*. The identity of *Littorina perdix* King & Broderip, 1832, is uncertain; no original material has been located in BMNH. The original diagnosis was inadequate, but the dimensions given (equivalent to 20.6×13.5 mm), together with the raised spiral striae, and white aperture with brown-spotted margin, support its synonymy with *L. varia*, and preclude all other South American littorinids. No locality was given; the title of the paper suggests that all specimens were collected on the South American voyages of the *Adventure* and *Beagle* between 1826 and 1830, neither of which visited the geographical range of *L. varia* (King, 1839). Nevertheless, in the same paper some species were also described from the Cuming and Sowerby collections, from localities such as Lima and Panama, which were not visited during these voyages. The identity of *Littorina perdix* with *L. varia* is therefore a possibility.

Diagnosis: Shell thick-walled; sculpture of strong spiral ribs; color whitish with minute brown flecks, aperture and columella white. Penis with small filament, large glandular disc on branch of base, unpigmented.

Shell (Figure 7A–C): Mature shell height 16–34.4 mm. Shape high-turbinate (H/B = 1.41–1.53, SH = 1.51–1.65); spire whorls only slightly rounded, sutures slightly channelled; angulation at periphery of last whorl marked by largest rib; thick-walled. Mature lip not flared; columella broad and hollowed. Sculpture of strong spiral ribs,

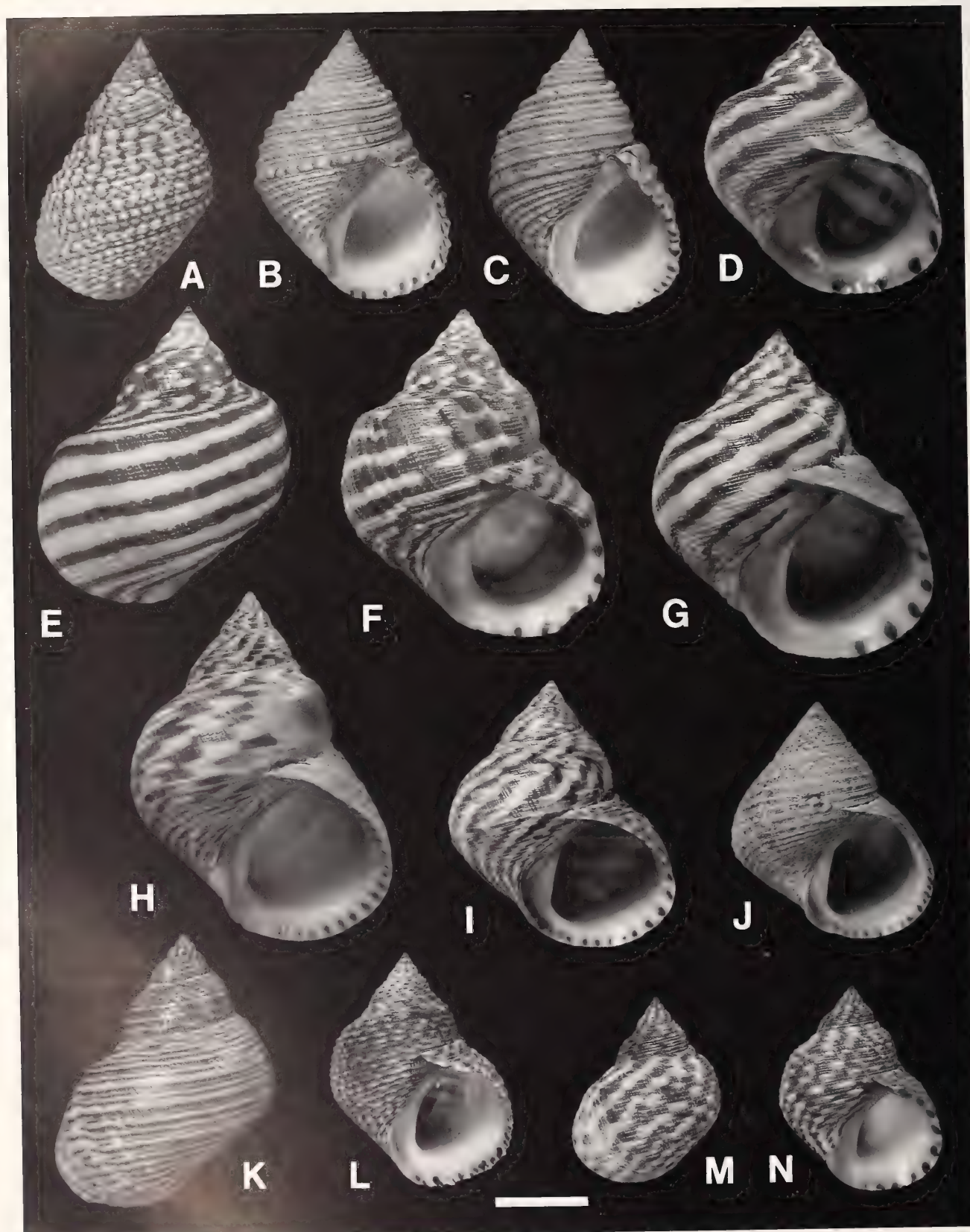
about 12–16 on last whorl, with one to two smaller cords in the broad spaces between each; axial growth lines distinct, especially near end of last whorl, giving slightly cancellate appearance between ribs; surface shiny, with only faint spiral microstriae; no discernible periostracum. Protoconch 0.31 mm diameter, about three whorls, terminated by sinusigera rib, sculpture not preserved. Color whitish to cream, closely and minutely flecked with dark brown; pattern sometimes aligned near suture to form close, narrow, axial stripes; pattern occasionally faint or absent. Columella and interior of aperture white; apertural margin marked with dark brown spots where pattern shows through.

Animal: Head, tentacles and sides of foot black; unpigmented stripe behind eye (Figure 2K). Opercular ratio 0.33–0.40. Hypobranchial gland exceptionally large, up to 3.0 mm wide in shell of 25.3 mm. Penis (Figure 2F, G, J) with large, wrinkled base and small smooth filament (15–20% total length); base bifurcate, broader branch bearing large, slightly pointed, glandular disc; sperm groove open (also anterior vas deferens from prostate), extending to tip of filament; unpigmented. Euspermatozoa 136 μ m; paraspermatozoa (Figure 3B, C) round to slightly oval, maximum diameter 21–26 μ m, packed with minute indistinct granules, one or two oval to elongate rod-pieces 4–17 μ m long. Pallial oviduct (Figure 4C) with spiral section of 5.5–6.5 whorls, of which capsule gland (with proximal opaque and distal translucent portion) is two whorls; bursa long, opening near anterior end of straight section of pallial oviduct, extending back to spiral section. Spawn and development not observed; presence of capsule gland suggests pelagic egg capsule; type of protoconch indicates planktotrophic development.

Radula (Figure 8A–E): Relative radular length 0.87–1.68. Rachidian: length/width 1.04–1.29; cusps extremely variable: one large rounded cusp with two pointed denticles on either side (Figure 8E), or five pointed cusps decreasing in size on either side of central cusp (Figure 8A), or central cusp may be short and blunt (Figure 8C); hood generally well developed, sometimes narrow. Lateral: four to six cusps, largest central cusp variable in shape and size (rounded, pointed or short and blunt); two to three small pointed cusps on inside and one to two on outside of main cusp. Inner marginal: three to four cusps, largest central cusp variable in shape and size (rounded, pointed or short and blunt); one to two small pointed cusps on inside and one on outside of main cusp. Outer marginal: two short broad cusps, either may be slightly larger, both bluntly rounded or pointed. Cusps of all teeth more elongate in smallest specimen examined (6.9 mm shell height), and three (not two) cusps on outer marginal.

Material examined: 40 lots; one protoconch; nine penes; four sperm samples; three pallial oviducts; seven radulae.

Habitat: At low levels on trunks and roots of mangroves,



only rarely on leaves, up to 2.1 m above ground; common from seaward edge to landward fringe (personal observation, Costa Rica); also on stones, logs, and grass among mangroves; muddy rocks on sheltered shores (Contreras & Cantera, 1978; Guerrini, 1990; personal observation). Remains at or below water level at high tide (Contreras & Cantera, 1978; Borjesson & Szelistowski, 1989).

Range (Figure 6B): Specimens seen from El Triunfo, El Salvador (13°34'N; USNM; also Hernandez, 1979, from 13°14'N) to Paita, Peru (5°11'S; USNM). The southern limit in Peru requires confirmation; Peña (1970, 1971b) records the species from Puerto Pizarro (3°34'S). Nevertheless, there is a relictual stand of mangroves at San Pedro (5°30'S), near Paita; although this species was not recorded in a survey of this site by Peña & Vásquez (1985), occurrence there may be possible, perhaps only during El Niño events when warm equatorial water extends this far south.

Remarks: Of the three large, common *L. (Littoraria)* species found in the mangroves of western Central America, *L. varia* occurs at the lowest levels on the trees (although there is considerable overlap among them), and is the only one that is regularly submerged by the rising tide (Peña, 1971a; Contreras & Cantera, 1978; Borjesson & Szelistowski, 1989; Blanco et al., 1995). In comparison with the higher-zoned *L. variegata*, the shell is thicker and the aperture more narrow. This makes it less susceptible to predators that forage during high tide, such as puffer fish, portunid and xanthid crabs, as shown by field tethering and laboratory predation trials (Borjesson & Szelistowski, 1989). The shells are nevertheless frequently damaged during unsuccessful predation attempts, and most specimens bear the evidence in the form of one or more scars of repaired breakages.

The intraspecific variation in the form of the radular tooth cusps is extreme. Radular variation has been described in other littorinid genera (e.g., *Bembicium* by Reid, 1988; *Littorina* by Reid, 1996), but *L. varia* is the most striking example. Although only seven radulae were examined, variation was evidently not correlated with sex, adult size, or locality. All specimens were from mangroves, so there was no obvious correlation with microhabitat (cf. *L. pintado pullata* described earlier). There

may, however, be ontogenetic change in radular form; cusps of all teeth were relatively longest (although not as pointed as in one adult), and on the outer marginal more numerous, in the smallest (6.9 mm) specimen available; similar trends have been documented in *Littorina* (Reid, 1996; see also description of *L. zebra*). As in other studies of radular variation in littorinids, it is notable that tooth cusps vary together in the same way; in particular the major cusp on each of the five central teeth of each row are always similar in shape, suggesting a developmental constraint.

There is a possibility of confusion among *L. varia*, *L. zebra*, and *L. variegata*, which are sympatric over much of their range (although *L. variegata* alone occurs in Mexico). *Littoraria varia* is easily recognized by the smaller apical angle of its more elongate shell, its pure white columella and interior of the aperture, sculpture of strong spiral ribs, the largest of which marks the angled periphery. *Littoraria zebra* is likewise thick-walled, but has a broader shell, distinctly angled at the shoulder, with bright coppery orange columella and inner apertural margin, and striking broad brown stripes on the final whorl. *Littoraria variegata* is thinner in texture, has rounded whorls, columella edged with brown, and a variable shell pattern (usually of narrow oblique stripes, zigzags, or spiral lines). Penial shapes are diagnostic of each. The copulatory bursa is similar in all three, but the spiral part of the pallial oviduct shows most numerous whorls in *L. variegata* and fewest in *L. varia*.

Littoraria (Littoraria) zebra (Donovan, 1825)

(Figures 2H, I, 3D, 4E, 6C, 7D–G, 8F–H)

Turbo zebra Donovan, 1825: pl. 130; caption to pl. 131 (Panama; lectotype (here designated) Donovan, 1825: pl. 130).

Littorina zebra—Morrison, 1946: 9. Keen, 1958: 282; fig. 179. Keen, 1971: 366; fig. 189. Guerrini, 1990: 14.

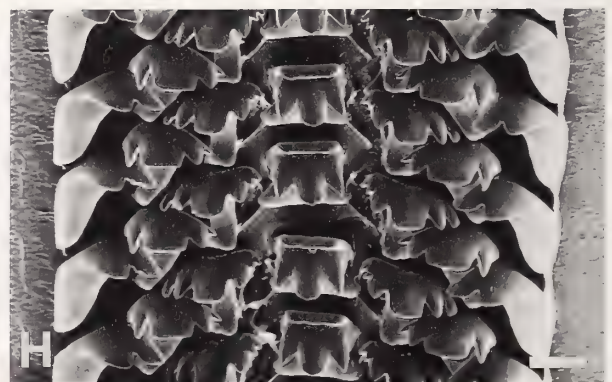
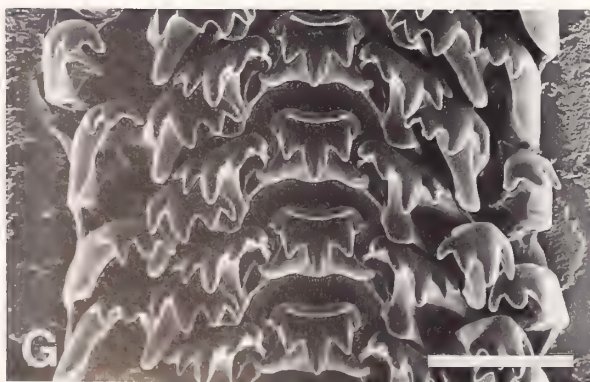
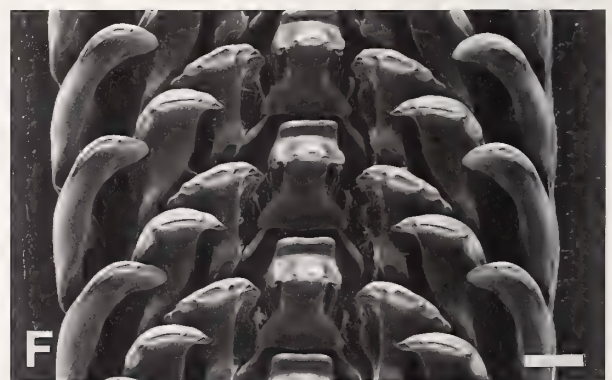
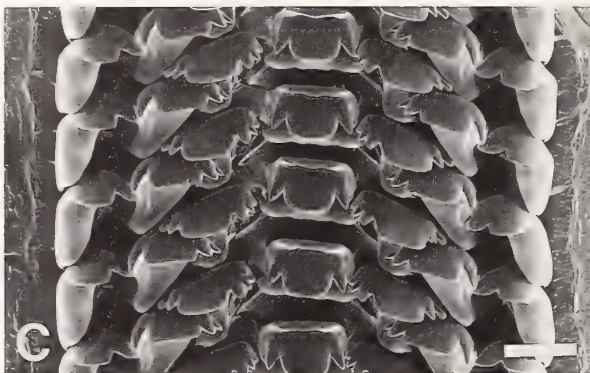
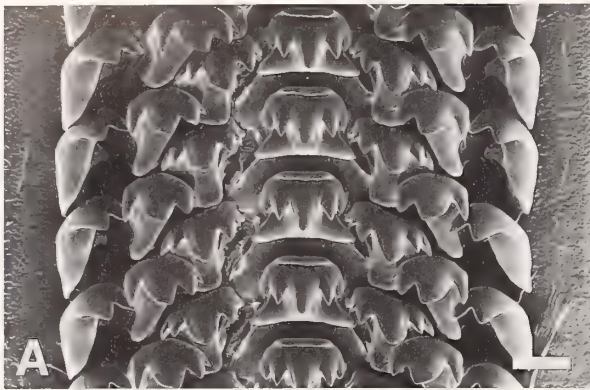
Littorina (Littoraria) zebra—Rosewater, 1970: 423; pl. 326, figs 6, 7.

Littoraria (Littoraria) zebra—Reid, 1986: 72; figs 41 (penis), 18 (cladogram), 99g. Reid, 1989: 97; pl. 2, fig. 2a; figs 7e (penis), 10c (oviduct), 14e (radula).

Littorina pulchra "Swainson" G. B. Sowerby, 1832: part 37; pl. 211, figs 2, 3 (no locality; types lost). Deshayes

Figure 7

Shells of *Littoraria varia* (A–C), *L. zebra* (D–G), *L. variegata* (H–K) and possible hybrids (L–N). A. Guayaquil, Ecuador (BMNH 1996200, Cuming Colln; note repaired crab breakage on penultimate whorl). B, C. Panama (BMNH 1967698, Cuming Colln). D. Puntarenas, Costa Rica (BMNH 1996201). E. Panama (BMNH 1996202). F, G. Panama (BMNH 1996203). H. El Salvador (BMNH 1996204; note eroded area where males attach in copulation position). I. Tumbes, Peru (BMNH 1996205). J. Lectotype of *Littorina variegata* Souleyet, in Eyedoux & Souleyet, 1852 (MNHN unregistered); La Puna, Guayaquil River, Ecuador. K. Tumbes, Peru (BMNH 1996206). L. Possible hybrid between *L. varia* and *L. variegata*; Puntarenas, Costa Rica (BMNH 1996154). M, N. Possible hybrids between *L. zebra* and *L. varia*; 2 miles west of Venado Beach, Veracruz, Panama (USNM 743087). Scale bar = 10 mm.



& Milne Edwards, 1843: 208. Adams, 1852: 399–400. Reeve, 1857: *Littorina* sp. 17; pl. 3, fig. 17a, b. Mörch, 1860: 68–69. Dall, 1909: 231. Pilsbry & Lowe, 1932: 124.

Littorina pulchra—Griffith & Pidgeon, 1834: 598; pl. 1, fig. 3.

Littorina pulchra—Philippi, 1846b: 2: 99; *Littorina* pl. 1, fig. 1. Weinkauff, 1882: 49–50; pl. 6, figs 6, 7.

Littorina (Melaraphe) pulchra—H. & A. Adams, 1854: 314. Tryon, 1887: 246; pl. 43, fig. 47.

Littorina (Littorinopsis) pulchra—von Martens, 1900: 581.

Littorina fasciata Gray, 1839: 139 (Pacific Ocean?; holotype BMNH 1968361, seen).

Taxonomic history: Until the resurrection of the earlier name by Keen (1958), this species was known by the name *pulchra*. The epithet *Littorina fasciata* Gray, 1839, has hitherto been incorrectly applied to the species here identified as *Littoraria variegata*. However, the synonymy with *L. zebra* is clearly indicated by Gray's description of "oblique transverse brown bands," "apex . . . purplish" and "whorls . . . concavely impressed near the suture"; furthermore, although this description was not accompanied by an illustration, the holotype in BMNH confirms the identification.

Diagnosis: Shell thick-walled; whorls shouldered; sculpture of fine spiral ribs; color orange with oblique brown stripes, aperture and columella orange. Penis with small filament, very large glandular disc on branch of blackish base.

Shell (Figure 7D–G): Mature shell height 16–40.6 mm. Shape turbate (H/B = 1.07–1.29, SH = 1.28–1.45); spire whorls rounded, sutures distinct; periphery of last whorl rounded, not angled; conspicuous angulation on shoulder of last whorl, resulting in square profile and flattened or concave area between shoulder and suture; thick-walled. Mature lip not flared, considerably thickened within; columella very broad (to 8 mm) and hollowed. Sculpture of numerous fine spiral ribs (36–44 on last whorl), evenly sized and separated only by incised lines; axial growth lines distinct, often giving ribs a minutely beaded appearance; fine spiral microstriae over whole surface if well preserved; periostracum not evident. Protoconch not clearly seen. Color coppery orange-brown, fading to cream, with striking pattern of broad chocolate brown stripes, forming oblique axial bands (7–12 at suture of last whorl) and zigzags, which tend to become spiral lines toward end of last whorl; spire whorls some-

times with a tessellated or reticulate pattern; apical two whorls of teleoconch purplish brown. Columella and aperture coppery orange; apertural margin marked with dark brown spots of external pattern.

Animal: Head, tentacles and sides of foot black, usually paler or unpigmented behind eye and at inside of tentacle base. Opercular ratio 0.36–0.40. Hypobranchial gland large, up to 1.5 mm wide in shell of 27.0 mm. Penis (Figure 2H, I) with wrinkled base and small smooth filament (20–30% total length); base bifurcate, bearing large, almost circular, glandular disc; sperm groove open (also anterior vas deferens from prostate), extending to tip of filament; filament unpigmented, base black, glandular disc grey. Euspermatozoa 195–200 µm; paraspermatozoa (Figure 3D) round to oval, maximum diameter 19–26 µm, packed with minute granules, one (rarely two to three) rectangular to oval rod-piece 5–18 µm. Pallial oviduct (Figure 4E) with spiral section of 7.5–8.5 whorls, of which capsule gland (with proximal opaque and distal translucent portion) is three whorls; bursa long, opening behind anterior end of straight section of pallial oviduct, extending back almost to spiral section. Spawn and development not observed; presence of capsule gland suggests pelagic egg capsule; type of protoconch indicates planktotrophic development.

Radula (Figure 8F–H): Relative radular length 1.16–2.02. Rachidian: length/width 0.97–1.32; cusps variable, central cusp largest, pointed to bluntly rounded, one pointed cusp and a denticle on either side; hood well developed. Lateral: five to six cusps, largest central cusp short and blunt, or rounded or pointed; two to three small pointed cusps on inside and two on outside of main cusp. Inner marginal: four cusps, largest central cusp short, broad and blunt, or longer and pointed; two smaller pointed cusps on inside and one on outside of main cusp. Outer marginal: two to four bluntly rounded cusps, outermost usually largest. All cusps relatively longest and most pointed in smallest specimen examined (shell height 8.2 mm).

Material examined: 28 lots; 14 penes; three sperm samples; six pallial oviducts; five radulae.

Habitat: On trunks and roots of mangroves, up to 2.0 m above ground; more common in middle zone of *Rhizophora* forest and landward fringe (personal observation, Costa Rica). Also on rocks, logs, and driftwood among

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Figure 8

Radulae of *Littoraria varia* (A–E) and *L. zebra* (F–H). A. Punta Morales, Golfo de Nicoya, Costa Rica (BMNH 1996213; at 45°; shell H = 25.2 mm). B–D. Puntarenas, Costa Rica (BMNH 1996219; three views of radula, flat, at 45° and at 45° from side; shell H = 30.2 mm). E. Punta Morales, Golfo de Nicoya, Costa Rica (BMNH 1996213; at 45°; shell H = 19.1 mm). F, H. Golfito, Costa Rica (BMNH 1996214; two views of radula, flat and at 45°; shell H = 27.0 mm). G. Golfito, Costa Rica (BMNH 1996214; at 45°; shell H = 8.2 mm; juvenile). Scale bars = 50 µm.

mangroves (Contreras & Cantera, 1978; Guerrini, 1990; personal observation). In Colombia, Contreras & Cantera (1978) reported that *L. zebra* avoids submersion by the high tide, and during low tide remains in the branches of the trees, overlapping with and above the zone occupied by *L. variegata*. In a study at Buenaventura Bay, Colombia, the mean tidal level of *L. zebra* was slightly above that of *L. variegata*, but the vertical ranges of each were almost the same (Blanco et al., 1995). At two sites in Costa Rica, there was also considerable overlap between these two species, but *L. variegata* attained higher levels (personal observation).

Range (Figure 6C): Specimens have been seen from between Playa Tamarindo, Costa Rica (10°19'N, BMNH) and San Lorenzo, Ecuador (1°17'N, USNM); literature records extend the range northward to Santa Elena Bay, Costa Rica (10°59'N; Pilsbry & Lowe, 1932) and southward to Bahía de Caráquez, Ecuador (0°38'S; Guerrini, 1990). Not reported from El Salvador by Zilch (1954).

Remarks: This spectacular species is the type of the genus *Littoraria*. For comparison with similar species, see Remarks on *L. varia*. Together with *L. variegata*, this species is gathered for food in Colombia, and is of potential economic importance (Cantera & Contreras, 1978).

As mentioned above, there is uncertainty about the relative vertical zonation of the two species *L. zebra* and *L. variegata*. In assemblages of *Littoraria* species on mangrove trees elsewhere in the tropics, the shells of species occupying lower tidal levels on the trees are more thick-walled, which has been related to the requirement for protection from crabs and other crushing predators that forage at lower levels (Reid, 1984, 1986, 1992; Cook et al., 1985; Borjesson & Szelistowski, 1989). It is therefore surprising that the shell of *L. zebra* appears considerably thicker and stronger than that of *L. variegata*, with which it shares a similar zonation. However, zonation levels are generally observed during diurnal low tide. In an Australian study, *Littoraria* species have been shown to be highly mobile, moving vertically on the trees with the rise and fall of the tide, particularly at night and dawn, and their zonation may also be influenced by rainfall and spawning (Reid, 1984). Prolonged observation is therefore necessary to establish relative patterns of zonation, and to discover whether species are exposed to predators. Interestingly, *L. zebra* seldom shows the scars of unsuccessful predation attempts on its shell, which are so common in *L. varia* (zoned at the lowest level on the trees).

Littoraria (Littoraria) variegata (Souleyet, in Eydoux & Souleyet, 1852)

(Figures 2D, E, L, 3E, F, 4D, 5F–H, 6D, 7H–K)

Turbo bicarinatus Wood, 1828: 20; pl. 6, *Turbo* fig. 47 (types lost; not Sowerby, 1825).

Littorina bicarinata—Mörch, 1860: 69.

Littorina fasciata—Philippi, 1847: 2: 221; *Littorina* pl. 5, figs 1, 2 (not *Littorina fasciata* Gray, 1839 = *Littoraria zebra*). Weinkauff, 1878: 40; pl. 4, fig. 11 (not Gray, 1839).

Littorina fasciata—Adams, 1852: 397 (not Gray, 1839). Reeve, 1857: *Littorina* sp. 20; pl. 4, fig. 20; pl. 18, fig. 103a, b (not Gray, 1839). Morrison, 1946: 9 (not Gray, 1839). Keen, 1958: 282; fig. 176 (not Gray, 1839). Keen, 1971: 366; fig. 182 (not Gray, 1839). Peña, 1971b: 47 (not Gray, 1839). Guerrini, 1990: 14 (not Gray, 1839).

Littorina (Melaraphe) fasciata—H. & A. Adams, 1854: 314 (not Gray, 1839).

Littorina (Littorinopsis) fasciata—von Martens, 1900: 580–581 (not Gray, 1839). Rosewater, 1970: 423 (not Gray, 1839). Abbott, 1974: 69 (in part, fig. is *Littoraria varia*; not Gray, 1839). Alamo & Valdivieso, 1987: 25 (not Gray, 1839).

Littorina (Algaroda) fasciata—Zilch, 1954: 80–81; pl. 3, fig. 7 (not Gray, 1839).

Littorina (Littoraria) fasciata—Reid, 1986: 72; figs 4n (penis), 18 (cladogram) (not Gray, 1839). Reid, 1989: 96 (not Gray, 1839).

Littorina variegata Souleyet, in Eydoux & Souleyet, 1852: 560; atlas pl. 31, figs 40–42 (la Puna, dans la rivière de Guayaquil [Ecuador]; lectotype (here designated, 25.9 mm; Figure 7J) + 1 paralectotype + 3 alcohol paralectotypes, MNHNP, seen).

Littorina (Melaraphe) varia—Tryon, 1887: 246; pl. 43, figs 45, 46 (in part, includes *Littoraria varia*; not Sowerby, 1832).

Littorina varia—Dall, 1909: 231, 285 (in part, includes *Littoraria varia*; not Sowerby, 1832).

Taxonomic history: Apparently following an initial misidentification by Philippi (1847), this species has been almost universally known by the name *L. fasciata*. However, *Littorina fasciata* Gray, 1839, is in fact a synonym of *L. zebra* (see Remarks on that species). The only available name for the present species is *L. variegata*. It is regrettable that this unavoidable name change, introduced here, may lead to confusion with *L. varia*.

Diagnosis: Shell of moderate thickness; whorls rounded; sculpture of fine spiral ribs; color cream variously patterned with brown flecks or stripes, aperture cream, edge of columella brown. Penis with unbranched, lightly pigmented base, incorporating glandular disc.

Shell (Figure 7H–K): Mature shell height 15–40.4 mm. Shape turbate (H/B = 1.14–1.44, SH = 1.35–1.53); spire whorls rounded, sutures distinct, not channelled; periphery of last whorl rounded, not angled, but sometimes marked by slightly enlarged rib; of moderate thickness. Mature lip not flared, thickened within as an indistinct rib; columella broad and hollowed. Sculpture of numerous fine spiral ribs, about 20 on last whorl, with three to five smaller riblets of varying size closely packed in the spaces between; axial growth lines often indistinct, but sometimes give ribs a finely beaded appearance; fine spiral microstriae over whole surface if well preserved; thin,

adherent periostracum. Protoconch 0.31 mm diameter, about three whorls, terminated by sinusigera rib, sculpture not preserved. Color whitish to cream or ochre, variously patterned with dark brown: fine flecks or dashes, sometimes merging into narrow spiral lines, but usually axially aligned to give 9–17 continuous oblique stripes, sometimes zigzags or coarse tessellation; pattern sometimes faint or absent. Edge of columella pale to dark brown, pillar cream; aperture cream to pale brown, pattern often showing through; apertural margin marked with dark brown spots of external pattern.

Animal: Head and tentacles dark grey, large unpigmented patch on inside of tentacle base, unpigmented stripe behind eye (Figure 2L); sides of foot flecked and lined with dark grey. Opercular ratio 0.43–0.47. Hypobranchial gland normal, up to 0.5 mm wide in shell of 20.3 mm. Penis (Figure 2D, E) with large, wrinkled base and small smooth filament (25–40% total length); base not bifurcate, bearing small, narrow, glandular disc distally; sperm groove open (also anterior vas deferens from prostate), extending to tip of filament; filament and glandular disc unpigmented, base with grey to blackish pigment in wrinkles, becoming darker basally. Euspermatozoa 255 μm ; paraspermatozoa (Figure 3E, F) round to elongate oval, maximum diameter 15–34 μm , packed with small granules, one (rarely two) rectangular to elongate rod-piece extending full length of cell. Pallial oviduct (Figure 4D) with spiral section of 8.5–9.5 whorls, of which capsule gland (with proximal opaque and distal translucent portion) is three whorls; bursa long, opening behind anterior end of straight section of pallial oviduct, extending back to spiral section. Spawn and development not observed; presence of capsule gland suggests pelagic egg capsule; type of protoconch indicates planktotrophic development.

Radula (Figure 5F–H): Relative radular length 1.41–2.14. Rachidian: length/width 1.07–1.31; cusps variable, central cusp largest, short and blunt, or rounded, one pointed cusp and usually a denticle on either side; hood generally well developed, sometimes narrow. Lateral: four to six cusps, largest central cusp short, broad and blunt; two to three small blunt or pointed cusps on inside and one to two on outside of main cusp; anterior face of tooth may be concave behind main cusp, so that inner and outer cusps are not aligned in same plane (Figure 5G). Inner marginal: four cusps, largest central cusp short, broad, and blunt; two small pointed cusps on inside and one on outside of main cusp. Outer marginal: two broad, bluntly rounded cusps, sometimes with small additional pointed cusp on outside.

Material examined: 56 lots; one protoconch; six penes; four sperm samples; five pallial oviducts; five radulae.

Habitat: On trunks, roots, and branches of mangroves, up to 2.5 m above ground; common throughout *Rhizophora* forest, from seaward edge to landward fringe (per-

sonal observation, Costa Rica). Sometimes also on muddy rocks on sheltered shores. This species climbs to avoid submersion by the high tide (Contreras & Cantera, 1978; Borjesson & Szelistowski, 1989). At two sites in Costa Rica it showed considerable overlap with *L. zebra* on the trees, but extended to higher levels (personal observation), although the reverse has been reported in Colombia (Contreras & Cantera, 1978; Blanco et al., 1995).

Range (Figure 6D): As first recorded by Carpenter (1857a) this species has a wide distribution. The known northern limits are Laguna Ojo de Liebre on the western coast of Baja California (27°45'N, USNM), La Paz (24°10'N, Pillsbury & Lowe, 1932) and Topolobampo in the Gulf of California (25°36'N, BMNH). Between Nayarit and El Salvador there is a gap of over 2000 km with no records, where the coastline is mainly of exposed rock and sand; here mangroves are largely restricted to enclosed brackish lagoons, in which *Littoraria* species are not known to occur (e.g., Stuardo & Villarroel, 1976). The southernmost record is from Puerto Pizarro, Tumbes, Peru (3°34'S; Peña, 1970, 1971b).

Remarks: This species is zoned at higher levels than *L. varia*, and unlike that species climbs to avoid submersion; correspondingly, its thinner shell is more susceptible to crushing by the predatory crabs and fish that forage in the mangroves during high tide (Borjesson & Szelistowski, 1989). Large female shells often show a smooth eroded patch on the penultimate whorl, presumably rasped by the radulae of males attached in this position during copulation. Although the shell is highly variable in coloration in the species as a whole, large samples from single localities show limited variability and cannot be described as polymorphic (a term strictly applied to discrete variation). Growth and allometry have been described by Cruz (1989), who detected no sexual dimorphism in size. For comparison with similar species, see Remarks on *L. varia*.

Possible hybrids of *Littoraria* species

(Figure 7L–N)

About 1300 shells of *L. varia*, *L. zebra*, and *L. variegata* have been examined during the present study, and almost all have been immediately identifiable because their shells are highly distinctive and show a narrow range of variability (at least in shape and sculpture). However, among them three specimens stand out, defying classification.

USNM 743087 (Figure 7M, N): The first two are present together with two typical *L. variegata* in a lot from “2 miles W of Venado Beach, Veracruz, Panama, NMNH-STRI Survey Stn 112, 5 Nov. 1972.” These two dry shells were first noted as possible hybrids in an annotation by J. Rosewater. Their dimensions are: H = 19.7 mm (H/B = 1.30; SH = 1.52); H = 22.7 mm (H/B = 1.30;

SH = 1.46). Both are thick-walled shells with internally thickened apertures indicating maturity. Superficially, shape and coloration resemble *L. variegata*; however, the shells are too solid and the spiral sculpture too coarse and regular. The sculpture is most like *L. zebra*, with closely spaced, minutely beaded, although somewhat irregularly sized spiral ribs; the broad columella is pale orange throughout (paler than in *L. zebra*, but not bordered with brown as in *L. variegata*). Internally, the apertural callus is white, a character found only in *L. varia*. In outline, the spire height is similar to that in *L. variegata*, but the last whorl is not uniformly rounded, but shows a slight angulation both at shoulder and periphery. External coloration is cream with a dark purplish brown pattern of coarse tessellation, aligned near the suture to form about 11 oblique stripes. It is tentatively suggested that these might be hybrids of *L. zebra* and *L. varia*.

BMNH 1996154 (Figure 7L): A third specimen was found together with typical forms of all three species in a *Rhizophora* forest at Puntarenas Yacht Club, Costa Rica (personal collection 5 December 1985). The shell outline is similar to the two shells described above (H = 25.4 mm; H/B = 1.32; SH = 1.45), but the texture is thinner and the lip not thickened. The sculpture is of numerous fine spiral ribs, but these are not crowded together or minutely beaded (as in *L. zebra*). Coloration is cream with a dark purplish brown pattern of small dashes, indistinctly aligned near the suture; the columellar pillar is white, the parietal callus and columellar edge ochraceous (as in *L. variegata*), and the internal callus of the aperture white (as in *L. varia*). The principal cusps of the five central teeth of the radula are short and blunt; there are three cusps on the outer marginal (not known in adult *L. varia*, but common in *L. variegata* and *L. zebra*). The head and sides of the foot are black; the hypobranchial gland is large (up to 1.9 mm wide); the ovary is not developed, but the pallial oviduct is well formed, with a spiral part of 6.5 whorls (of which the capsule glands occupy three). Unfortunately, the female reproductive tract is not as clearly diagnostic of species as the male, but the characters listed appear to combine, or are intermediate between, those of *L. varia* and *L. variegata*. Conceivably this specimen could be a hybrid between these two.

Remarks: In the absence of genetic evidence, this suggestion of hybridization must remain tentative. It is clear that these three specimens show combinations of characters that are sufficiently unusual that they are probably not simply aberrant examples of one or other of the three large mangrove-dwelling *Littoraria* species. Alternatively, they might represent an additional undescribed species. This seems less likely, for two reasons. The thickness, sculpture, and columellar color of the two collections are sufficiently different that it could be doubted that they are conspecific. Secondly, if one (or even two) ad-

ditional large *Littoraria* species were present in the mangroves of Costa Rica and Panama, it is improbable that it would be represented by so few specimens among the large collections available from these areas. However, the possibility cannot be dismissed, and further material should be sought. Hybrids between littorinid species have been claimed from morphological evidence only once before; this was the case of intermediates between *Nodilittorina australis* (Gray, 1826) and *N. nodosa* (Gray, 1839) reported by Rosewater (1970); these two are now known to belong to a single variable species (Reid, 1989). This explanation is quite clearly untenable in the present examples. Since the copulatory behavior of male littorinids is somewhat indiscriminate, interspecific copulation attempts have often been observed in the field (see Reid, 1986: 59–61 for *Littoraria* species; Reid, 1996: 14–15 for review in *Littorina* species). Attempts have been made to hybridize closely related *Littorina* species in the laboratory, but almost all have failed (Warwick et al., 1990; Boulding et al., 1993). The only successful example of laboratory hybridization so far reported was between *Littorina saxatilis* (Olivier, 1792) and *L. arcana* Hannaford Ellis, 1978, and even then no hybrids were detected in natural populations by allozyme electrophoresis (Warwick et al., 1990). If natural hybrids do occur, they are likely to be extremely rare. Conceivably, however, the case of the three large *Littoraria* species in the Eastern Pacific might provide a system in which rare natural hybrids could be more readily recognized. Most littorinid sister-species are so similar in shell morphology that natural hybrids are unlikely to be conspicuous in the field. The anatomical similarities of these three Eastern Pacific species suggest recent divergence (cladogram of Reid, 1989), and yet each has a highly distinctive shell morphology, so that large numbers of individuals can quickly be scanned for aberrant examples. Further anatomical and genetic investigation of this possibility would be of interest.

Littoraria (Littoraria) rosewateri Reid, sp. nov.

(Figures 3G, H, 6E, 9A–D, 10D, 11A–E, K, L)

Littorina debilis—Morrison, 1946: 9–10 (not Philippi, 1846, a synonym of *Nodilittorina ziczac* (Gmelin, 1791); based on USNM 588870, seen).

Littorina aberrans—Keen, 1971: 365; fig. 179 (in part; includes *Littoraria aberrans* (Philippi, 1846)).

Littorina scabra aberrans—Rosewater, 1980b: 158–162; figs 11, 12 (radula) (in part; other figs are *Littoraria aberrans* (Philippi, 1846)).

Littoraria (Littoraria) n. sp. Reid, 1986: 73; figs 4k (penis), 18 (cladogram).

Types: Holotype BMNH 1996155 (Figure 9B), 11 paratypes in alcohol BMNH 1996156, one paratype USNM 880187 (Figure 9A). Type locality: Topolobampo, 20 km west of Los Mochis, Sinaloa, Mexico.

Etymology: This species is named in memory of the late Joseph Rosewater, who had a special interest in the Littorinidae, and contributed much to the understanding of their systematics (see Rehder, 1986, for tribute and bibliography).

Taxonomic history: Hitherto, this species has generally been misidentified as *L. aberrans* (e.g., Keen, 1971) or included with it (Rosewater, 1980b). It was noted as an undescribed species by Reid (1986).

Diagnosis: Shell small, elongate, solid; last whorl rounded; protoconch 0.30 mm diameter. Penis with large filament containing closed sperm duct; glandular disc on branch of base. Pallial oviduct with capsule gland, indicating spawning of pelagic eggs.

Shell (Figure 9A–D, 10D): Mature shell height 5–12.3 mm. Shape elongate ($H/B = 1.70$ – 1.86 , $SH = 2.00$ – 2.44); spire whorls rounded, sutures distinct; last whorl uniformly rounded, sometimes a slightly enlarged rib at periphery; of moderate thickness. Mature lip not flared, but previous lips may be visible as strong growth interruptions near end of final whorl; columella narrow, not hollowed, pinched at base, with slight convex bulge above. Sculpture of incised spiral lines, five to eight visible on spire whorls (Figure 10D), increasing to 17–45 at end of last whorl; lines sometimes obsolete on last whorl; axial growth lines indistinct on spire whorls, but may become conspicuous on last whorl; surface shining, without spiral microstriae; periostracum thin, adherent. Protoconch (Figure 10D) 0.30–0.31 mm diameter, about three whorls, terminated by sinusigera rib, sculpture poorly preserved, but five to six spiral ribs visible. Color polymorphic; ground color cream to pale yellow brown, or pale pinkish orange; variable development of brown pattern; usually of smudged spots or dashes on ribs, aligned near suture and periphery to form short axial stripes or series (8–16 on last whorl), but pattern sometimes absent. Columella and parietal callus purplish brown in patterned shells, otherwise pale orange brown; aperture pale yellowish brown or pinkish orange, external pattern showing through.

Animal: Head grey to black, pale at tip of snout, tentacles pale with transverse grey lines; unpigmented patch at inside of tentacle base and behind eye; sides of foot pale grey or speckled with black (Figure 11A). Opercular ratio 0.45–0.46. Penis (Figure 11B–E) with wrinkled, bifurcate base bearing rectangular glandular disc; filament large (50% total length), constricted at base, tapering; sperm duct closed (also anterior vas deferens from prostate), opening at tip of filament; penis unpigmented, filament sometimes pale reddish orange in life. Euspermatozoa 62–72 μm ; paraspermatozoa (Figure 3G, H) round to oval, maximum diameter 10–14 μm ; packed with large spherical granules; single, narrow rod-pieces 18–24 μm , projecting from cells. Pallial oviduct (Figure 11K, L) with

spiral section of 3.5–4.5 whorls, of which capsule gland (with proximal opaque and distal translucent portion) about 1.5 whorls; bursa small, opening near anterior end of short straight section of pallial oviduct. Spawn and development not observed; presence of capsule gland suggests pelagic egg capsule; type of protoconch indicates planktotrophic development.

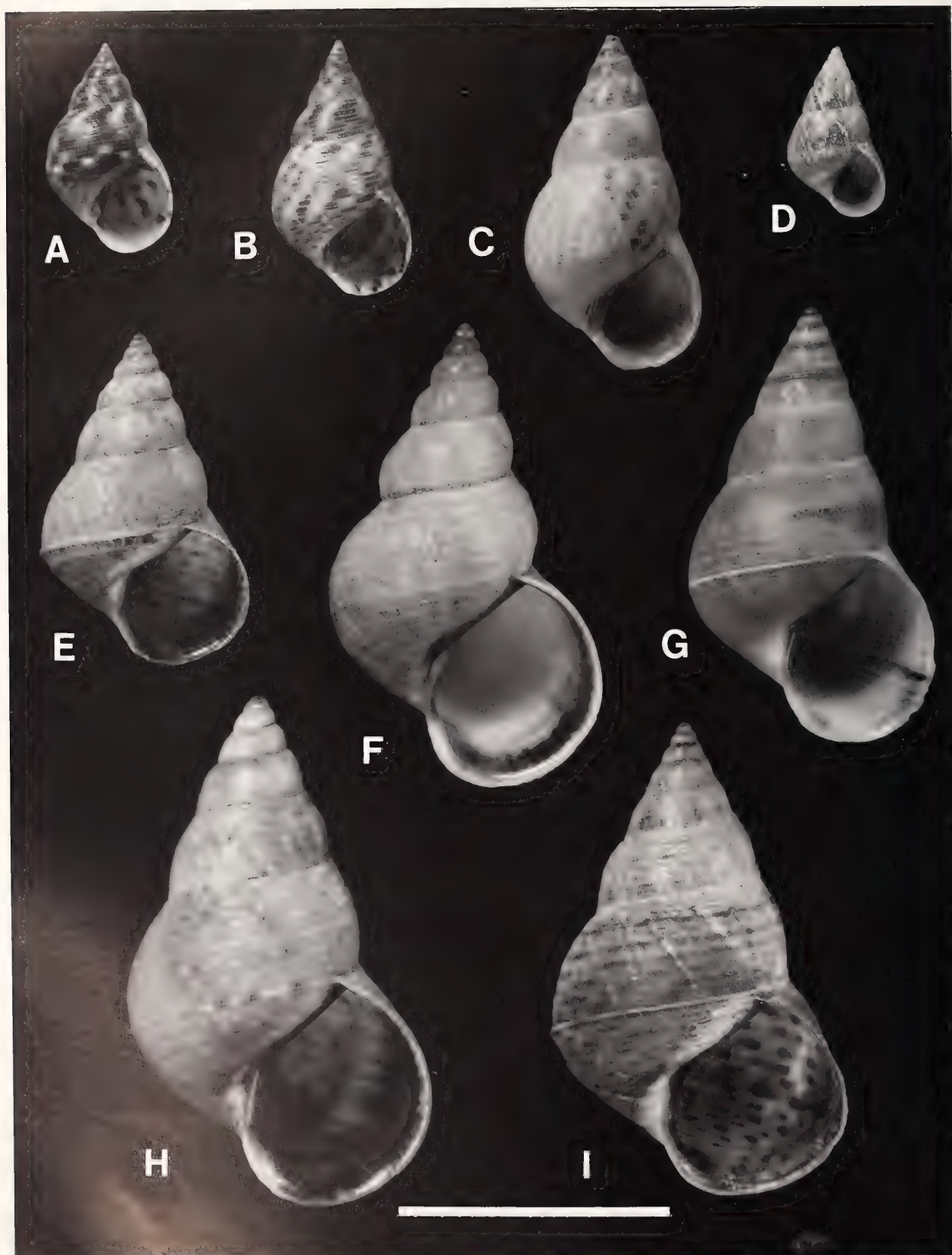
Radula (Figure 12A–E): Relative radular length 0.90–1.67. Rachidian: length/width 0.95–1.21; central cusp largest, usually pointed, sometimes bluntly rounded, one pointed cusp and usually a denticle on either side; hood well developed. Lateral: five to six cusps, largest central cusp pointed or bluntly rounded; two to three smaller pointed cusps on inside and one to two on outside of main cusp. Inner marginal: four cusps, largest central cusp pointed or rounded; two smaller pointed cusps on inside and one on outside of main cusp. Outer marginal: four to six pointed cusps, outermost largest.

Material examined: Types; 19 lots; two protoconchs; seven penes; seven sperm samples; five pallial oviducts; six radulae.

Habitat: Abundant among grass and sedge tussocks in salt marshes; on and under boulders in littoral fringe on sheltered muddy shores; on leaves and branches of mangroves (*Avicennia*). Typically at edges of brackish lagoons, creeks, or near freshwater seepages on shore. Morrison (1946) reported it as extremely abundant on rotting coconut fronds, in drift behind the sand barrier at the mouth of a swamp.

Range (Figure 6E): This species has a wide range, although available records are few. On the west coast of Baja California it has been found at Bahía Magdalena (24.5°N, USNM), and frequently on the eastern shore of the Gulf of California, from Puerto Peñasco (29°59'N, LACM) to Topolobampo (25°36'N, BMNH). There is then an apparent gap of over 3000 km, where much of the coastline is of exposed sand and rock; there are, however, brackish lagoons with mangrove vegetation where the species might be found (although molluscan diversity is low in such habitats, e.g., Stuardo & Villarroel, 1976). There are several records from Costa Rica and Panama, and the most southerly record is from Puerto Pizarro, Peru (3°30'S, LACM).

Remarks: This species has probably often been overlooked because of its small size and unusual habitat at the highest tidal levels on shores and in salt marshes. When it has been collected, it has previously been confused with *L. aberrans*. The two are easily distinguished: *L. rosewateri* is smaller in size, more solid, the spire usually relatively taller, and the small protoconch is of the planktotrophic type (cf. large protoconch of few whorls indicating nonplanktotrophic development in *L. aberrans*); characters of the reproductive anatomy are diagnostic.



Subgenus *Bulimilittorina* Reid, 1989**Type species:** *Littorina aberrans* Philippi, 1846**Diagnosis:** Development nonplanktotrophic with intracapsular metamorphosis; penis bifurcate, base containing two long, coiled, glandular structures opening at pair of papillae; capsule gland absent in pallial oviduct; embryos brooded in mantle cavity, released as crawling young (diagnosis after Reid, 1989).*Littoraria* (*Bulimilittorina*) *aberrans* (Philippi, 1846)

(Figures 3I, 6F, 9E–I, 10A–C, E–G, 11F–J, 12F–H)

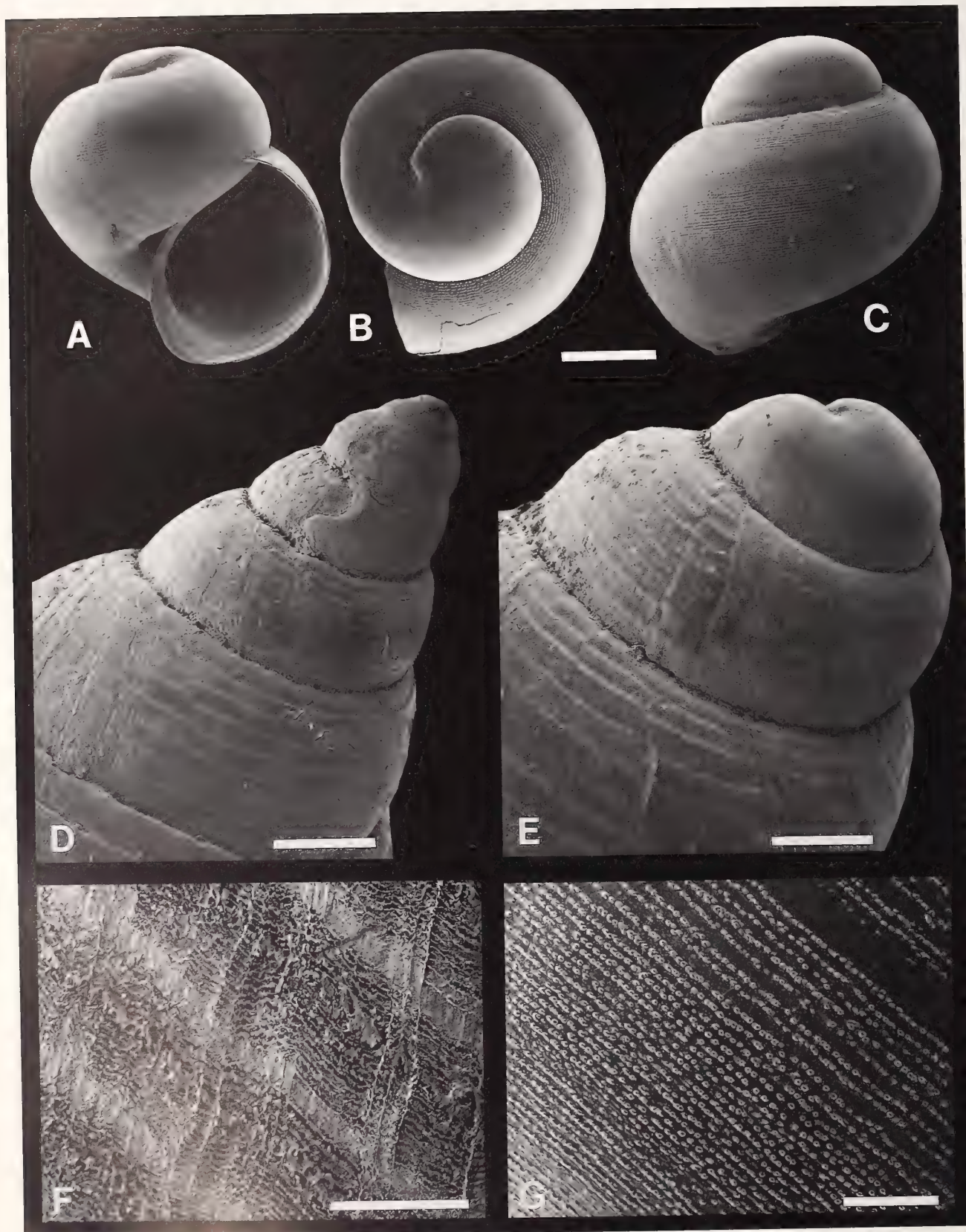
Littorina? *aberrans* Philippi, 1846a: 142–143 (Panama; holotype BMNH 1968325, seen; Figure 9F).*Littorina aberrans*—Philippi, 1847: 3: 11; *Littorina* pl. 6, fig. 9. Weinkauff, 1882: 72–73; pl. 9, fig. 13.*Littorina aberrans*—Reeve, 1857: *Littorina* sp. 59; pl. 12, fig. 59. von Martens, 1900: 587–588. Keen, 1971: 365 (in part; fig. is *Littoraria rosewateri*).*Littorina* (*Littorinopsis*) *scabra aberrans*—Rosewater, 1970: 423.*Littorina scabra aberrans*—Rosewater, 1980b: 158–162; figs 3, 6 (in part; other figs. are *Littoraria rosewateri*).*Littorina* (*Melaphe*) *aberrans*—Tryon, 1887: 245; pl. 43, fig. 32.*Littoraria aberrans*—Reid, 1986: 14, 73, 77–79; fig. 18 (cladogram).*Littoraria* (*Bulimilittorina*) *aberrans*—Reid, 1989: 14, 28, 31, 38, 42, 85–86, 97–98; figs 7h (penis), 10f (oviduct), 14h (radula), 15 and 16 (cladograms).*?Littorina glabrata*—Morrison, 1946: 9 (not Philippi, 1846 = *Littoraria glabrata*).**Taxonomic history:** In the original description, Philippi (1846a) doubtfully referred this species to *Littorina*, remarking on the resemblance to the terrestrial pulmonate *Bulimus*, and this uncertainty persisted (Tryon, 1887; von Martens, 1900). Throughout the nineteenth century this species was known only from the holotype (Philippi, 1847; Reeve, 1857; Tryon 1887; von Martens, 1900), and since then *L. aberrans* has been figured only by Rosewater (1980b) and Reid (1989).**Diagnosis:** Shell elongate, delicate; last whorl sometimes

keeled at periphery; mature lip slightly flared; protoconch 0.68 mm diameter. Penis with large filament containing open sperm groove; base contains two large tubular glands, opening at two papillae on side branch. Pallial oviduct without capsule gland. Ovoviviparous; mantle cavity packed with embryos in brooding females.

Shell (Figure 9E–I, 10A–C, E–G): Mature shell height 9–18.7 mm; marked sexual dimorphism in size, largest male 12.0 mm. Shape high-conical (H/B = 1.58–1.76, SH = 1.87–2.15); spire whorls gently or well rounded, sutures distinct; periphery marked by sharp, keeled rib in juveniles, often becoming indistinct on last whorl which is then uniformly rounded; thin-shelled and delicate. Mature lip slightly flared, and if growth is resumed may occasionally remain as a single varix; columella a simple narrow pillar, slightly pinched at base, becoming detached in largest shells to give slight pseudoumbilicus. Sculpture of 8–11 weak incised spiral lines on spire whorls (Figure 10E); on last whorl developing into 21–33 weak, narrow, rounded ribs; peripheral rib is a sharp keel in juveniles and some adults; periostracum prominent for the genus; fine periostracal ridges (Figure 10F) appear at low magnification as microstriae over whole surface; axial growth lines marked by slight periostracal flanges; rarely, growth lines are prominent and numerous on last whorl, intersecting with spiral ribs to give indistinctly cancellate appearance. Protoconch (Figure 10A–C, E) 0.68 mm diameter, 1.8 whorls, terminated by straight growth line; first whorl smooth, then sculptured by numerous rows of minute (3 µm diameter) tubercles, developing first near suture (Figure 10G). Color polymorphic; ground color cream to pale brownish yellow; variable development of brown pattern: usually a rather regular checkered pattern of small dashes or spots on ribs, sometimes aligned in axial series (11–20 on last whorl), or uniformly finely mottled if spots are small, but pattern sometimes absent; color often varies with growth: brown at apex, pattern pale or absent on spire whorls, then darker on last whorl, and most intense just behind lip. Columella, parietal callus, and aperture near lip dark purplish brown in patterned shells, cream or pale brown in unpatterned shells.**Animal:** Head and tentacles dark grey to black, pale at tip of snout; tentacles indistinctly banded, unpigmented

Figure 9

Shells of *Littoraria rosewateri* Reid, sp. nov. (A–D) and *L. aberrans* (E–I). A, B. Paratype (A; USNM 880187) and holotype (B; BMNH 1996155) of *Littoraria rosewateri* Reid, sp. nov.; Topolobampo, 20 km west of Los Mochis, Sinaloa, Mexico. C. East end of causeway to Medanos Blancos, Sinaloa, Mexico (LACM 120157). D. Golfito, Costa Rica (BMNH 1996207). E. Punta Morales, Golfo de Nicoya, Costa Rica (BMNH 1996208). F. Holotype of *Littorina aberrans* Philippi, 1846 (BMNH 1968325); Panama. G. Farfan River, Panama (USNM 380676). H. Farfan Beach, Panama (USNM 380675). I. Punta Morales, Golfo de Nicoya, Costa Rica (BMNH 1996208). Scale bar = 10 mm.



patch at inside of tentacle base and sometimes behind eye (Figure 11F); sides of foot mottled with black. Opercular ratio 0.48–0.50. Penis (Figure 11G–I) with wrinkled, bifurcate base bearing two short papillae with blunt, puckered openings in place of glandular disc; two large, convoluted, tubular glands visible by transparency, extending from papillate openings to very base of penis; filament large (40–60% total length), tapering; open sperm groove (also anterior vas deferens from prostate), extending to tip of filament; penis largely unpigmented, base faintly grey. Euspermatozoa 120 μm ; paraspermatozoa (Figure 3I) round, 9–13 μm diameter, surface minutely rough, contents indistinctly granular, no obvious rod-pieces. Pallial oviduct (Figure 11J) with spiral section of 2.5–3.5 whorls, capsule gland absent; bursa short, opening near anterior end of long straight section of pallial oviduct. Development ovoviviparous, with intracapsular metamorphosis; in brooding females mantle cavity is solidly packed with embryos; one female (17.6 mm) contained 600 unencapsulated embryos, all at same stage of development, shell diameters 0.65–0.68 mm (Figure 10A–C). Gill leaflets similar in gross appearance to those in other members of genus; in a female of 15.0 mm, width of gills (from hypobranchial gland to osphradium) 4.0 mm, maximum height of leaflets 0.5 mm.

Radula (Figure 12F–H): Relative radular length 0.64–0.74. Rachidian: length/width 1.11–1.47; central cusp largest, with mucronate point, one pointed cusp and a denticle on either side; hood well developed. Lateral: seven cusps, largest central cusp square; four short pointed or rounded cusps on inside and two small pointed cusps on outside of main cusp; anterior face of tooth is concave behind main cusp, so that inner and outer cusps are not aligned in same plane. Inner marginal: five to seven cusps, largest blunt; three to five smaller pointed cusps on inside and one on outside of main cusp. Outer marginal: four to five cusps, outermost pointed, others bluntly rounded; neck and base of tooth unusually broad.

Material examined: Type; 12 lots; two protoconchs; 10 embryonic shells; five penes; two sperm samples; three pallial oviducts; four radulae.

Habitat: Leaves, branches and roots of *Rhizophora* at

landward edge of mangrove forests, up to 3.5 m above ground; apparently always scarce.

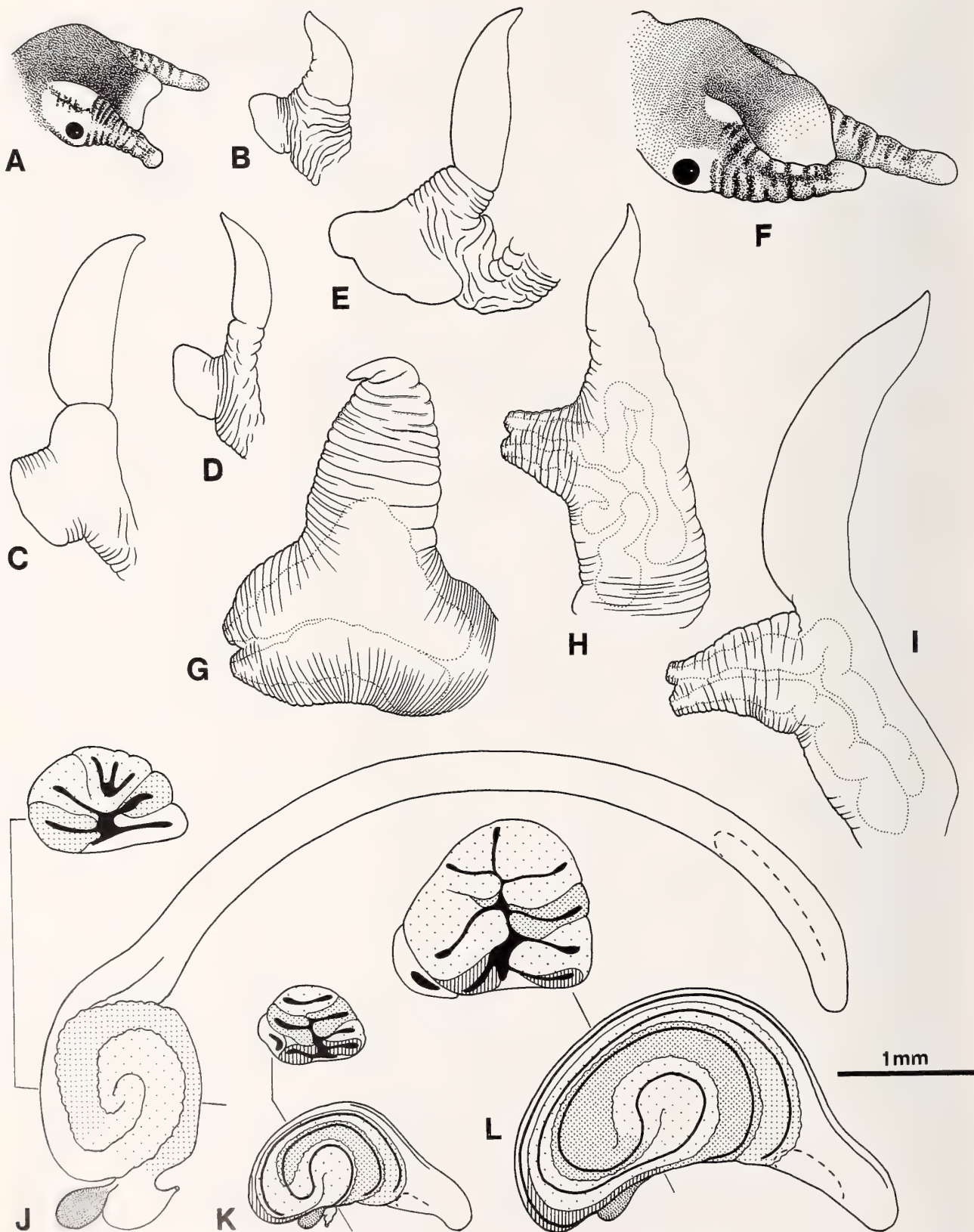
Range (Figure 6F): The few available records are from Playa Tamarindo (10°19'N, BMNH), Puntarenas, and Quepos, all in Costa Rica, and Farfan River, Taboga Island and San José Island (8°15'N, USNM), all in Panama. Since the species is uncommon and occurs at high tidal levels, it may have been overlooked elsewhere. "*Littorina scabra aberrans*," mentioned from the branches and foliage of mangroves in Colombia (Blanco et al., 1995), may refer to this species (or perhaps to *L. rosewateri*), but has been described as "very abundant" (Cantera et al., 1983).

Remarks: This species is the only member of the genus, and one of only four species in the family (Reid & Geller, 1997), to show ovoviviparity with intracapsular metamorphosis, so that crawling juveniles are released from the female. Twelve other species of *Littoraria* (the members of the subgenus *Littorinopsis*) are also ovoviviparous, but in these the larvae are released from the mantle cavity as planktotrophic early veligers with shells about 0.1 mm in diameter (Reid, 1986). Assuming that ovoviviparity has arisen only once in *Littoraria*, the condition in *L. aberrans* has presumably been derived from that shown by *Littorinopsis* species (Reid, 1989). Elimination of the marine larval stage is presumably adaptive in this species which inhabits such high levels in the trees, often at the landward fringe of mangrove forests where contact with the tide is infrequent, making it effectively a terrestrial snail. This type of development might be expected to be advantageous for other *Littoraria* species which occupy a similar high-level habitat elsewhere in the tropics; however, its absence may perhaps be explained by the consequent limitation of larval dispersal, which increases the likelihood of extinction (Reid & Geller, 1997). In immature or non-brooding females, ovoviviparous development is still recognizable because of the absence of capsule glands (and consequently small spiral section) in the pallial oviduct.

Another anatomical peculiarity of this species is the unique structure of the penis. All other species of the genus possess a glandular pad or sucker, the penial gland-

Figure 10

SEM details of shells of *Littoraria aberrans* (A–C, E–G) and *L. rosewateri* Reid, sp. nov. (D). A–C. Unencapsulated juveniles of *L. aberrans* from mantle cavity of brooding female; Punta Morales, Golfo de Nicoya, Costa Rica (BMNH 1996218). D. Apex and protoconch of *L. rosewateri* Reid, sp. nov.; Golfito, Costa Rica (BMNH 1996217). E. Apex and protoconch of *L. aberrans*; Punta Morales, Golfo de Nicoya, Costa Rica (BMNH 1996218). F. Detail of sculpture and periostracum on last whorl of *L. aberrans*; Punta Morales, Golfo de Nicoya, Costa Rica (BMNH 1996218). G. High-power detail of sculpture of larval shell of *L. aberrans*; Punta Morales, Golfo de Nicoya, Costa Rica (BMNH 1996218). Scale bars: A–E = 200 μm ; F = 400 μm ; G = 50 μm .



dular disc (although this is not clearly differentiated in the basal species *L. pintado*). The tubular glands of *L. aberrans* are superficially similar to the mamilliform penial glands of other Littorininae, but their histology and staining reactions suggest that they are not homologous, and have probably been formed by infolding of the penial glandular disc (Reid, 1989).

The delicate shell of *L. aberrans*, with flared aperture, is similar to those of the members of the subgenus *Littorinopsis* that likewise inhabit high supratidal levels among the foliage of mangrove trees (Reid, 1986). A study of the behavior of this virtually terrestrial species would be interesting, for it is likely that it rarely comes into contact with the high tide (see Reid, 1984, for account of the behavior of Australian *Littoraria* species). Consequently it avoids the powerful predators such as fish and crabs that forage at lower levels on the trees during high tide, and a thick protective shell is unnecessary (Reid, 1992). The pigmentation of the shell is variable, and this is apparently a true polymorphism, since both unpigmented and variously patterned shells can be found together. However, none corresponding to the orange-pink morph of other polymorphic *Littoraria* species have yet been seen. Shell color polymorphism in *Littoraria* is associated with a habitat among the foliage of mangrove trees (Reid, 1986), and the color polymorphism of both *L. rosewateri* and *L. aberrans* strengthens this correlation. It is believed to be maintained by visual selection against the varied background, and may be adaptive in relation to predation (Cook, 1983, 1986, 1992; Hughes & Mather, 1986; Reid, 1987; Cook & Garbett, 1992).

This species is one of the rarest littorinids in museum collections. This is not simply the result of its limited geographical distribution, for it appears always to be genuinely scarce in its mangrove habitat. This is in contrast to the high abundance attained by some other foliage-dwelling *Littoraria* species (Reid, 1985). The holotype was for long the only specimen known; this shell (Figure 9F) is an aberrant example with exceptionally rounded

whorls, narrow spire, and fine spiral ribs. This partly explains the early doubt about its generic allocation (Philippi, 1846a; Tryon, 1887; von Martens, 1900), for this shell does closely resemble some terrestrial prosobranchs of the genus *Chondropoma* Pfeiffer, 1847. Nevertheless, the protoconch, sculpture of the early whorls, columella, and dark pigmentation around the aperture are sufficient to identify it with others of the species, and intermediates with rounded last whorls (Figure 9H) connect it with the more typical form with keeled periphery and less marked sutures (Figure 9E, G, I).

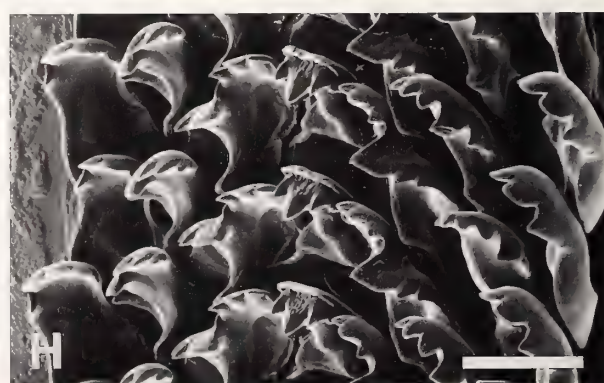
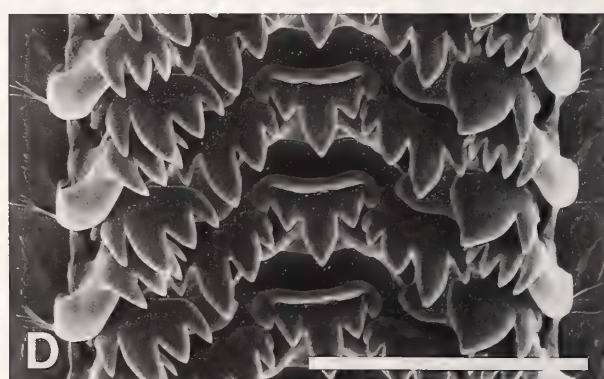
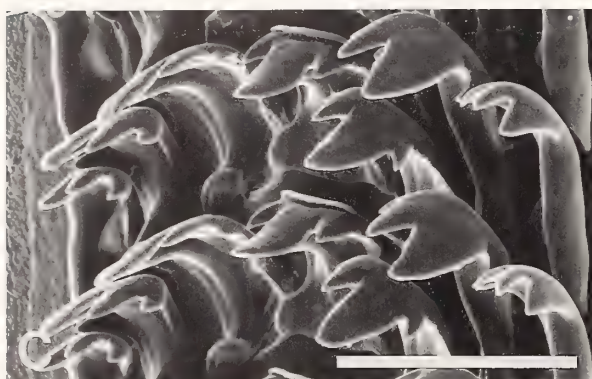
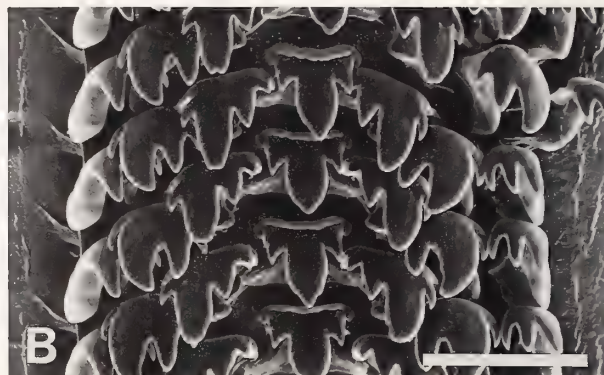
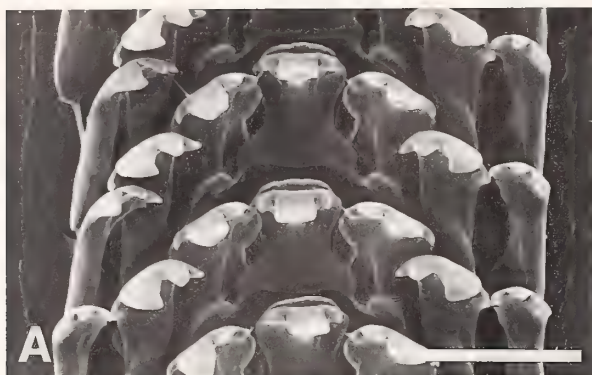
Among other *Littoraria* species in the Panamic province, confusion is only likely with *L. rosewateri* (see Remarks on that species). In the absence of accurate locality information, confusion could easily arise with *L. angulifera* (Lamarck, 1822) from the Caribbean coast of Central America. That species reaches larger size (36 mm), is generally a broader, more solid shell with more rounded whorls, and the columella, while narrow, is excavated; most importantly the sculpture is finer (50–90 ribs on last whorl, cf. 21–33 in *L. aberrans*), and the protoconch is of the planktotrophic type (0.35 mm diameter, about 3 whorls, sinusigera rib). Anatomically, the penis of *L. angulifera* has a bifurcate base bearing a glandular disc and a large filament (Reid, 1986: fig. 4o), and in the female the mantle cavity contains numerous small eggs and embryos that are brooded only to the early veliger stage with shells about 0.1 mm in diameter.

DISCUSSION

The evolutionary history of the marine species of Central America has long been of particular interest, because of the opportunity for the study of processes of speciation and extinction that is provided by the Pliocene emergence of the Isthmus of Panama (review by Vermeij, 1993). Until recently, it was believed that the formation of the land bridge about 3 million years ago not only isolated the Eastern Pacific and Western Atlantic provinces, but also caused an episode of extinction that was most severe in

Figure 11

Anatomy of *Littoraria rosewateri* Reid, sp. nov. (A–E, K, L) and *L. aberrans* (F–J). A. Head of *L. rosewateri* Reid, sp. nov.; Golfito, Costa Rica (BMNH 1996217). B–E. Penes of *L. rosewateri* Reid, sp. nov. B, D. Golfito, Costa Rica (BMNH 1996217; shell H of B = 5.1 mm; shell H of D = 4.7 mm). C. Penis of paratype of *L. rosewateri* Reid, sp. nov.; Topolobampo, Sinaloa, Mexico (BMNH 1996156). E. Rio Marina Lagoon, San José Island, Pearl Islands, Panama (USNM 588870). F. Head of *L. aberrans*; Punta Morales, Golfo de Nicoya, Costa Rica (BMNH 1996218). G–I. Penes of *L. aberrans*; Punta Morales, Golfo de Nicoya, Costa Rica (BMNH 1996218; shell H of G = 12.0 mm; shell H of H = 9.1 mm; shell H of I = 9.7 mm; penis G is in a more contracted state than H and I; tubular glands visible by transparency are indicated by dotted outlines). J. Pallial oviduct of *L. aberrans*; Punta Morales, Golfo de Nicoya, Costa Rica (BMNH 1996218; shell H = 17.0 mm). K. Pallial oviduct of *L. rosewateri* Reid, sp. nov.; Golfito, Costa Rica (BMNH 1996217; shell H = 6.0 mm). L. Pallial oviduct of paratype of *L. rosewateri* Reid, sp. nov.; Topolobampo, Sinaloa, Mexico (BMNH 1996156; shell H = 9.3 mm). Shading conventions as in Figure 4.



the Atlantic, resulting in an impoverished Caribbean fauna (e.g., Vermeij & Petuch, 1986). It now appears that the extinctions began later, about 2.4 million years ago, perhaps as a result of changing patterns of upwelling and productivity (Jackson et al., 1993). Furthermore, extinctions were balanced by speciation and immigration, so that the overall diversity of Caribbean mollusks has not decreased since the Pliocene, and is not lower than that of the tropical Eastern Pacific (Allmon et al., 1993). The modern differences between the faunas of these two provinces are therefore the result not only of differential patterns of extinction, but also of origination. Unfortunately, neither the phylogenetic relationships nor fossil history of *Littoraria* are yet sufficiently well known to permit more than speculation on its evolutionary history in Central America.

The genus *Littoraria* has a pantropical distribution, and the oldest fossils occur in the Lower Eocene of France (Reid, 1989). Of the 36 Recent species, 25 occur in the Indo-West Pacific province. This compares with the six species reported here from the Eastern Pacific, five from the Western Atlantic and two from the Eastern Atlantic (Reid, 1986). The Western Atlantic species are *L. angulifera* (Lamarck, 1822), *L. flava* (King & Broderip, 1832), *L. irrorata* (Say, 1822), *L. nebulosa* (Lamarck, 1822), and *L. tessellata* (Philippi, 1847). On the basis of shell resemblance, Rosewater (1963) suggested the following pairs of "species analogues" on either side of the Isthmus of Panama: *L. varia* and *L. irrorata*, *L. pintado* and *L. tessellata*, *L. fasciata* and *L. angulifera*. However, shells are a poor guide to affinity among littorinids, and (with the possible exception of the first) none of these pairs is supported by anatomical evidence. Later, using both shell and radular characters, Rosewater (1980b) classified *L. scabra* (L.) as a single pantropical species, with subspecies *L. s. scabra* in the Indo-West Pacific, *L. s. angulifera* in the Atlantic, and *L. s. aberrans* in the Eastern Pacific, but again anatomical evidence has contradicted the implied relationships (Reid, 1986). In an early attempt to use biochemical characters to define "geminant species pairs" on either side of Panama, Jones (1972) analyzed allozyme frequencies and myoglobin banding patterns in 12 littorinids, but failed even to separate the generic groupings now recognized as *Littoraria* and *Nodilittorina*, much less to identify consistent species-pairs. Reid (1986) used a cla-

distic analysis of anatomical characters to define basal groups within *Littoraria*, and relied on subjective assessment of shell and penial form to suggest terminal groupings; on this basis the only close relationships of species across the Isthmus were among *L. varia*, *L. zebra*, *L. variegata*, and *L. irrorata*.

The present redescription of the *Littoraria* species of the Eastern Pacific has partly supported this earlier study. *Littoraria pintado* has no known sister-species among living members of *Littoraria*, and its subspecies, *L. p. pulcata* is probably a relatively recent, Pleistocene, arrival in the Eastern Pacific from the west. The three species *L. varia*, *L. zebra*, and *L. variegata* are believed to form a clade, sharing likely synapomorphies of similar oviducts (tightly wound spiral; anterior bursa) and radulae (narrow posterior base of rachidian; only two to three cusps on outer marginal). This close relationship is also supported by the possible hybrids between them, discussed earlier. If they are indeed recently diverged from a common ancestor, their diversity of penial form is noteworthy, suggesting that the size of the glandular disc and degree of bifurcation of the base are readily modified, and might be species-recognition characters. Elsewhere in the genus, the same combination of radular and oviduct characters is found only in the Western Atlantic species *L. irrorata* (also exhibiting a non-bifurcate penis similar to that of *L. variegata*), which may therefore belong to the same clade. These four American species were linked by Reid (1986) with the Indo-West Pacific *L. vespacea* Reid, 1986, but reexamination of its radula has shown that it does not share the same characters. The new species *L. rosewateri* shares the synapomorphy of the closed penial vas deferens with the two Caribbean species *L. flava* and *L. tessellata* (these are likely sister-species, sharing a uniquely elongated penial filament, although the base is bifurcate only in the latter). Radular characters are also similar among these three, as is the overall form of the pallial oviduct. However, the bursa opens in an anterior position in *L. rosewateri*, posteriorly in *L. flava*, and is variable in position in *L. tessellata*; this character may not be phylogenetically informative in these species with a relatively short straight section of the pallial oviduct (as also suggested in *Littorina*, Reid, 1996: 349). The penial glands and intracapsular metamorphosis of *L. aberrans* are unique in the genus; its ovoviviparity is a synapo-

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Figure 12

Radulae of *Littoraria rosewateri* Reid, sp. nov. (A–E) and *L. aberrans* (F–H). A–C. Radula of paratype of *L. rosewateri* Reid, sp. nov.; Topolobampo, Sinaloa, Mexico (BMNH 1996156; three views of radula, flat, at 45° and at 45° from side; shell H = 9.3 mm). D, E. Golfito, Costa Rica (BMNH 1996217; two views of radula, at 45° and flat; shell H = 6.0 mm; note aberrant inner marginal teeth on right side, with only two cusps). F–H. Punta Morales, Golfo de Nicoya, Costa Rica (BMNH 1996218; three views of radula, at 45°, flat and at 45° from side; shell H = 17.6 mm). Scale bars = 50 µm.

morphy shared with the subgenus *Littorinopsis*. No characters have yet been found which might indicate its relationships more precisely, and there is no reason to suppose that it is the sister-species of the Atlantic *L. (Littorinopsis) angulifera*. A reanalysis of the relationships of *Littoraria* species, using additional information on radular characters, is in progress.

The trans-Panamanian relationships discussed above are mostly different from those predicted from shell characters (Rosewater, 1963, 1980b). The lack of phylogenetically significant shell characters suggests that the fossil record may not be very helpful in reconstructing the evolutionary history of *Littoraria*. The pre-Pleistocene record of this genus in Central America is meager: two specimens of "*Littorina varia*" from the Pliocene of California (Hanna, 1926), three specimens of "*Littorina angulifera*" from the Miocene of Panama and Costa Rica (Woodring, 1957), and numerous records of *L. irrorata* from the Upper Miocene and Pliocene of Florida, North and South Carolina (e.g., Smith, 1936; Bequaert, 1943). These will be examined in future work.

During the emergence of the Panama land bridge, separation of Pacific and Atlantic populations of all marine species did not take place simultaneously. Those able to tolerate inshore conditions appear to have remained in genetic contact until the final stages of the imposition of the barrier (Knowlton et al., 1993), which is estimated to have occurred about 3.2 to 2.5 Ma (Coates et al., 1992). It is likely that the *Littoraria* species of mangrove environments, tolerant of turbidity and reduced salinity, were among the last to be separated. The absence of any obvious pairs of sister-species on either side of the modern isthmus is therefore surprising, and suggests that subsequent speciation, extinction, or migration may have obscured the expected pattern. It is also possible that there was already some differentiation of Pacific and Atlantic faunas before the isthmus appeared (Vermeij, 1993). For comparison, populations of *Littorina squalida* Broderip & Sowerby, 1829, in the Northern Pacific and Northern Atlantic were isolated about 4 to 2.4 Ma (as a result of climatic cooling following opening of the Bering Strait), and the resulting pair of sister-species, *L. squalida* and *L. littorea* (Linnaeus), are clearly recognizable on morphological grounds (Reid, 1996); this pair of planktotrophic developers has not undergone further speciation during this time. In contrast, the trans-Panamanian relationships discussed above suggest that some speciation may have occurred over a similar time scale, in these likewise planktotrophic *Littoraria* species (e.g., *L. varia*, *L. zebra*, *L. variegata* in the Eastern Pacific; *L. flava* and *L. tessellata* in the Caribbean). However, this remains to be investigated by further phylogenetic and paleontological work.

The geographical distributions of the Eastern Pacific *Littoraria* species clearly show limitation by habitat. *Littoraria pintado pullata* is restricted to oceanic high is-

lands (although current patterns may have prevented its colonization of the Galápagos Islands); on the American mainland it occurs commonly only at the extremity of Baja California. The remaining five species are all found predominantly among mangrove vegetation. The southern limits of three of these (*L. varia*, *L. variegata*, *L. rosewateri*) coincide with the southern limit of mangroves, in northern Peru, whereas that of *L. zebra* is a little farther north. Northern limits are less well established owing to a paucity of information about El Salvador and Guatemala, but the long stretch of coastline without coastal mangroves between southern Mexico and the Gulf of California appears to present a barrier to *L. varia* and *L. zebra*. Only *L. variegata* and *L. rosewateri* occur to the north of this barrier, thus showing markedly disjunct ranges. Although egg capsules have not yet been described, all these five species have planktotrophic development (indicated by protoconch and capsule glands), with the corresponding potential for wide larval dispersal. Rafting might also be a common means of dispersal in the mangrove-associated species. Only the sixth species, *L. aberrans*, has non-planktotrophic development, which might partly explain its restricted distribution.

Bequaert (1943) reported that the Caribbean species *L. angulifera* had reached the Pacific coast of Panama through the Panama Canal. However, this has not been confirmed by the extensive museum collections from this area examined during the present study. The record may perhaps have arisen from confusion with *L. aberrans*.

Among the mangrove-associated *Littoraria* species of the Indo-West Pacific, interspecific trends in shell architecture and coloration, at successive levels on the trees, have been explained as adaptive responses to gradients in crushing and visual predation; species zoned at lower levels are thick-shelled and monomorphic, those found at higher levels are thinner-shelled, and those inhabiting the foliage are thinnest, and often color polymorphic (see Introduction). As discussed in the Remarks on each species, these trends are also apparent in the Eastern Pacific, although *L. zebra* is somewhat anomalous.

The "hooded" type of rachidian tooth is found in most *Littoraria* species, including all those known to occur on trees, driftwood and marsh plants, which led to the suggestion that it might be adaptive for grazing on such substrates (Rosewater, 1980a; Reid, 1986, 1989). However, the new discovery that a small "hood"-like structure is also be present in some examples of the basal, rock-dwelling, species *L. pintado* suggests that it might perhaps be a synapomorphy of the genus, lost in a few species. Little is known about the diet of *Littoraria* species, but a mangrove-associated species (*L. angulifera*) and a salt-marsh species (*L. irrorata*) both include a significant component of fungal material in their diets (Kohlmeyer & Bebout, 1986; Newell & Bärlocher, 1993; Bärlocher & Newell, 1994). The intraspecific variation in form of the tooth cusps in *L. varia* (and to a lesser extent in *L. va-*

riegata and *L. pintado pullata*) is the most remarkable example in the family. Such extreme variation has not previously been found in *Littoraria* species (Reid, 1986), but has been reported in other littorinid genera (Reid, 1988, 1996; Padilla, 1998).

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Genetic and Environmental Control of Growth and Reproduction of *Phacosoma japonicum* (Bivalvia: Veneridae)

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Abstract. The venerid bivalve *Phacosoma japonicum* (Reeve, 1850) shows north-south gradients in the annual shell growth and sexual maturity patterns among the Japanese populations. However, one southern population from Ariake Bay, Kyushu, does not fit with this general trend, and life-history traits of this population are comparable to those of the northern population in Hakodate Bay, Hokkaido. In this study, to understand the genetic and environmental factors responsible for the life-history traits of this species, transplant experiments and analyses of monthly shell growth and reproductive cycles were conducted on the populations from Ariake Bay and its neighboring regions. A total of 128 living individuals were transplanted from the population in Tokyo Bay (central Japan) and those in Ariake and Kagoshima Bays (southwestern Japan) to Aburatsubo Cove, Sagami Bay (central Japan). Follow-up studies of the transplanted individuals for 3 years revealed that both annual and seasonal shell growth patterns of most individuals did not differ from those of animals in the habitats of origin. This fact suggests that the mode of shell growth of this species is not only controlled by environmental factors but also has some genetic background. Analysis of the seasonal patterns of growth and reproductive cycles revealed that shell growth and gonad development were active from winter to early spring in individuals from Ariake Bay, whereas growth and reproduction occurred from late spring to summer in individuals from Tokyo and Kagoshima Bays. Seasonal changes in water temperature and salinity and also population density were similar among Ariake Bay and its neighboring regions. However, phytoplankton becomes most abundant in winter in Ariake Bay, in contrast to most other bays of central and southern Japan, including Tokyo and Kagoshima Bays, where phytoplankton flourishes in summer. These facts suggest that the growing seasons for both shell growth and reproduction of this species are strongly influenced by the annual pattern of food availability, and the geographical variations of annual shell growth and sexual maturity patterns can be explained by the difference in mean water temperature during the growing season among them.

INTRODUCTION

Many bivalve species exhibit geographic variation in life-history patterns (e.g., Taylor, 1959; Ansell, 1968; Gilbert, 1973; Appeldoorn, 1983; Tanabe & Oba, 1988; Sato, 1994), and a number of studies have discussed controlling environmental factors such as temperature (Green & Hobson, 1970; Noda et al., 1995), salinity (McLusky & Allan, 1976), food availability (Beukema et al., 1977; Thompson & Nichols, 1988; Irlandi & Peterson, 1991; Nakaoka, 1992), and density effects (Rae, 1979; Broom, 1982; Peterson, 1982). Recently, there have been theoretical studies which explain how life-history traits have evolved by natural selection (Roff 1992; Stearns 1992). However, life-history traits are not usually adaptive to their environment (Futuyma 1986). For example, variation in life-history traits may be caused by genetic drift. In this situation, life-history traits are not influenced by environmental factors at all. On the other hand, life-history traits

may not be genetically programmed, but instead may be a direct consequence of environmental controls. In this case, traits are not inherited by the descendants, so they never cause life-history evolution. Therefore, in order to understand the life-history evolution of organisms, it is important to elucidate both environmental and genetic factors.

The venerid bivalve *Phacosoma japonicum* (Reeve, 1850) is a common intertidal to subtidal species along the coasts of Japan, Korea, and China (Habe, 1977). Life-history traits of this species have been analyzed in detail (Tanabe, 1988; Tanabe & Oba, 1988; Sato, 1994, 1995), and a progressive change in life-history traits along a north-south gradient has been observed. Northern populations generally exhibit more delayed sexual maturity and larger shell size at a given age than the southern ones. However, one southern population from Ariake Bay, Kyushu, does not fit this general trend. Age of sexual maturity and maximum shell size of the population in Ariake Bay are comparable to those of the northern population in Hakodate Bay, Hokkaido (Figure 1). Because the genetic distance between the Ariake and Hakodate populations is much greater than those between popula-

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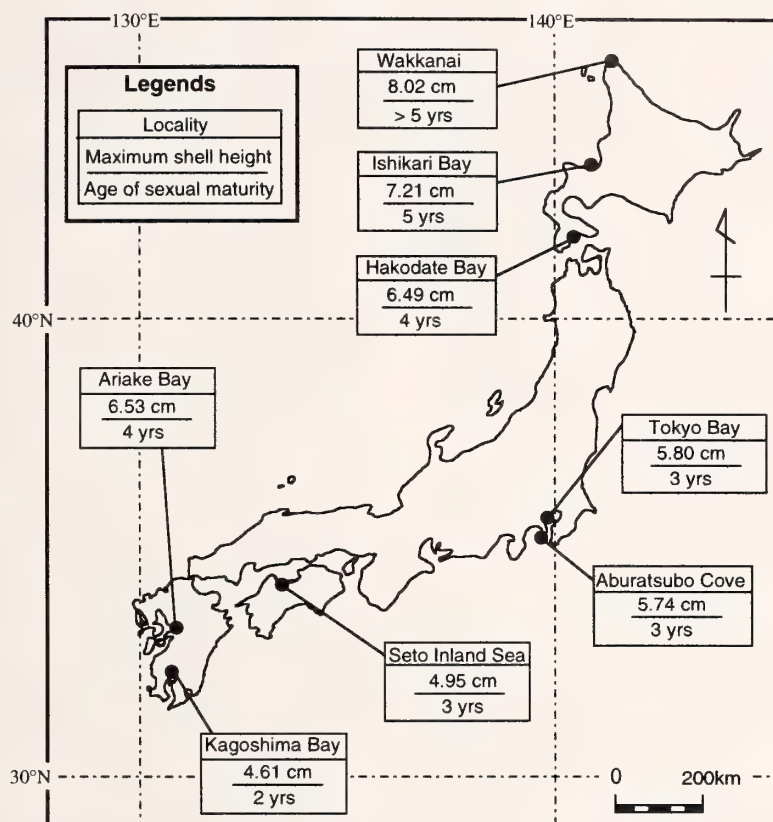


Figure 1

Sampling locations and life-history traits in each local population of *Phacosoma japonicum*. Numbers in box are maximum asymptotic shell height determined by the Bertalanffy equation (upper) and age of sexual maturity (lower), which were analyzed by Sato (1994).

tions in Ariake Bay and its neighboring regions (Sato, 1996), the aberrant life-history traits in the Ariake population cannot be explained solely by phylogenetic restrictions such as genetic drift.

In this study, to reveal the factors responsible for the variations in the life-history traits of this species, I attempted to estimate their genetic and environmental backgrounds by transplant experiments and analysis of monthly shell growth and reproductive cycles for the populations from Ariake Bay and its neighboring regions.

MATERIALS AND METHODS

Transplant Experiments

Transplant experiments were carried out on the intertidal sand flat of Aburatsubo Cove, Sagami Bay, central Honshu (35°9'20"N, 139°36'55"E). A total of 128 living individuals (2 to 4 years old) of *Phacosoma japonicum* were collected by digging with hands in April 1992 from the intertidal sand flat of (1) Nojima Coast, Tokyo Bay, central Honshu; (2) Nagahama Coast, Ariake Bay, central

Kyushu; and (3) Shigetomi Coast, Kagoshima Bay, southern Kyushu (see Figure 1 for sampling localities).

Each individual was tagged with a plate with an identification number, and transplanted at several sites in the intertidal zone of Aburatsubo Cove. Shell height of each individual was measured annually between April 1992 and April 1995, and those of the 2 year old individuals measured bimonthly from April 1992 to October 1992 with a slide caliper (accuracy ± 0.05 mm), and shell growth trajectory after transplantation was analyzed.

Seasonal Patterns in Growth and Reproduction

Seasonal changes in shell growth and reproductive cycle were examined for the native individuals from Tokyo, Ariake, and Kagoshima Bays. Thirty to forty individuals were sampled monthly from Ariake and Kagoshima Bays from January to September, 1995. Data on individuals from Tokyo Bay during January to October, 1992 are from Sato (1995). Gonadal tissue in each individual was excised and weighed using a dial scale (accuracy ± 10

mg). Then the dissected gonadal tissue was fixed for 48 hours in a solution of 10% formalin buffered with seawater, followed by dehydration through a graded series of ethanol and benzols, and then embedded in paraffin (melting point: 58°C). Thin transverse sections of the gonadal tissue were prepared at intervals of 8 μm thickness and were stained with hematoxylin-eosin. The stained thin sections were subsequently observed using an Olympus model AHBS-515 optical microscope.

Based on histological examination of thin-sectioned gonads, each individual was assigned to one of the specific gonad developmental stages (early active [EA], late active [LA], ripe [R], partially spawned [PS], spent [S]) as previously defined by Sato (1995) (see Sato, 1995: figs. 1, 2). The frequency of each stage in monthly samples provided data on the temporal progression of the reproductive cycle. In addition, I calculated the mean gonad index percentage gonad mass to total mass of soft tissue for sexually mature individuals every month.

The seasonal changes of shell growth were analyzed based on the annual increments produced by winter breaks (cf. Tanabe, 1988). Shell height from the umbo to the ventral margin of each winter break was measured using a slide caliper to an accuracy of ± 0.05 mm. Subsequently, net growth (x), defined as the increase of shell height in the period from the time of the last winter break to the month of sampling, was standardized for each individual by the expected annual growth (y), defined as the distance from the last winter break to the expected next winter break (cf. Goshima & Noda, 1992). The percentage of the ratio x/y is defined as the "growth index" (Sato, 1995).

The extent of the expected annual growth (y) for each individual was estimated using the Ford-Walford equation (Ford, 1933; Walford, 1946). The equation is expressed as

$$H_{R+1} = aH_R + b,$$

where H_R is the shell height at the R th winter break (in mm), H_{R+1} is the shell height at the $R+1$ th winter break (in mm), and a and b are constants determined by a simple regression between H_R and H_{R+1} of different individuals of the same sample. Using this equation, shell height at the expected next winter break of each individual (H_{R+1}) can be estimated by shell height at the last winter break (H_R) and constants at each age class (a, b).

Environmental Conditions of Each Locality

Data of seasonal changes of water temperature, salinity, and contents of chlorophyll a near the sampling localities were quoted from the unpublished data of the Tokyo Metropolitan Office (Tokyo Bay), of the Kagoshima Environmental Research and Service (Kagoshima Bay), and of the Kumamoto Prefectural Fisheries Research Station (Ariake Bay). Seasonal patterns of shell growth and

reproductive cycle of *Phacosoma japonicum* were compared with the environmental data, and then the factors that directly influenced the life-history traits of this species were analyzed.

RESULTS

Transplant Experiments

Annual shell growth patterns of the individuals of the four populations in the original localities and those of the transplanted individuals are shown in Figure 2. The mean shell growth pattern of the native individuals in Tokyo Bay is very similar to that in Aburatsubo Cove, but those in Kagoshima and Ariake Bays show earlier and later decline of shell growth than the individuals in Aburatsubo Cove, respectively (Sato, 1994).

The annual shell growth patterns of most individuals transplanted from Tokyo Bay to Aburatsubo Cove were quite similar to those of the native individuals in Tokyo Bay and Aburatsubo Cove (Figure 2a). However, annual shell growth rate of the individuals transplanted from Kagoshima and Ariake Bays to Aburatsubo Cove decreased at an earlier and later age than the native individuals in Aburatsubo Cove, respectively. Individuals transplanted from Kagoshima Bay attained the maximum shell size at 4 or 5 years old (Figure 2b). Most of the individuals transplanted from Ariake Bay continued to grow larger after 6 years old in contrast to the native individuals in Aburatsubo Cove (Figure 2c). The annual shell growth patterns of most transplanted individuals resembled those of the native individuals in their populations of origin.

Mean bimonthly shell growth rate from April 1992 to October 1992 in the 2 year old transplanted individuals is shown in Figure 3. The shell growth of the individuals transplanted from Tokyo and Kagoshima Bays to Aburatsubo Cove occurred mainly from June to October, but shell growth in individuals transplanted from Ariake Bay to Aburatsubo Cove was observed during April and August (Figure 3). As mentioned, shell growth was active from winter to early spring in the native individuals from Ariake Bay, but growth occurred from late spring to summer in the native individuals from Tokyo and Kagoshima Bays (see Figure 5b). These results indicate that most transplanted individuals attaining 2 years of age from the three geographically isolated habitats did not show any marked differences in both annual and seasonal shell growth patterns from those in their original habitats.

Seasonal Patterns of Reproduction and Growth

Seasonal variation in the frequency of each phase in the reproductive cycles of *Phacosoma japonicum* collected from Tokyo, Kagoshima, and Ariake Bays is shown in Figure 4. The reproductive cycle of the sample from Kagoshima Bay was similar to that from Tokyo Bay. In contrast, gonad development in individuals from Ariake

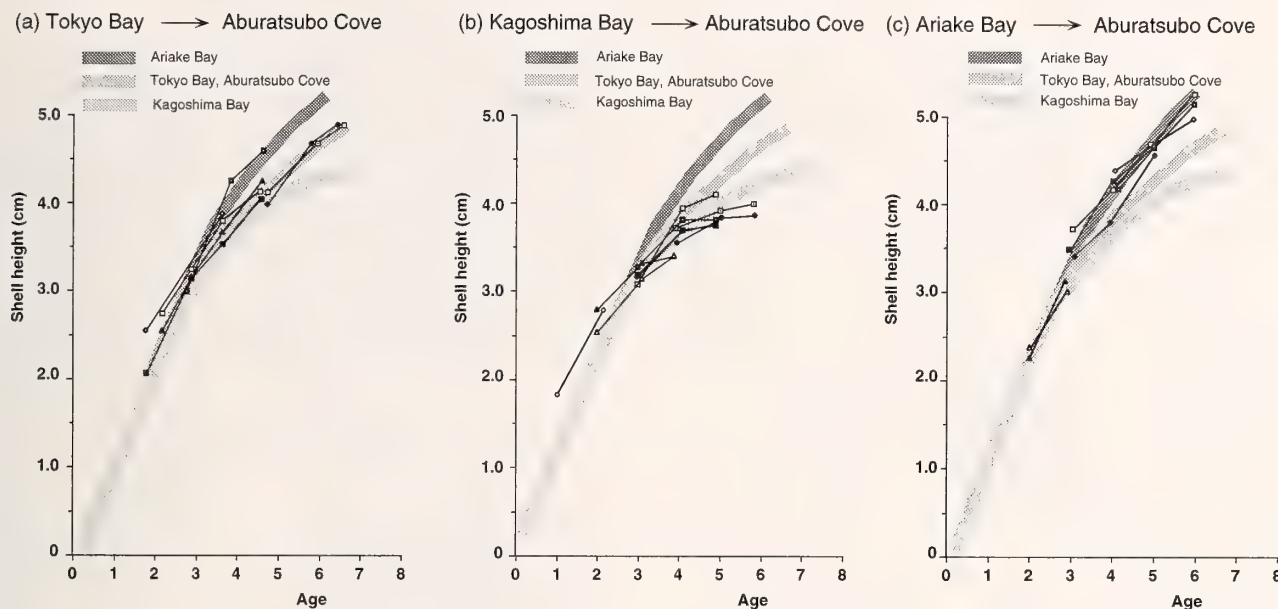


Figure 2

Results of the transplant experiments in Aburatsubo Cove. Each line represents annual shell growth trajectory of different individual transplanted from Tokyo Bay (a), Kagoshima Bay (b), and Ariake Bay (c). Bold lines indicate averaged annual shell growth patterns of the samples from the four original populations.

Bay occurred earlier. Namely, ripe individuals appeared between March and April in Ariake Bay, whereas they occurred after May in Tokyo and Kagoshima Bays (Figure 4). Some individuals also started to spawn in early June in Ariake Bay, but in Tokyo and Kagoshima Bays, spawning was delayed until July to August. The mean gonad index of the sample from Ariake Bay had already increased at a high rate (more than 40%) until April (Figure 5a). In contrast, in the samples from Tokyo and Kagoshima Bays, it increased at a lower rate (less than 40%) during January to April, and then increased rapidly in May and June.

The growth index of each individual in the samples from Tokyo, Kagoshima, and Ariake Bays was calculated based on the constants of Ford-Walford equation at each age class. The seasonal patterns of growth index showed that at Ariake Bay the rate of increase in shell height was rapid from February to April, but declined from April to July (Figure 5b). In contrast, at Tokyo and Kagoshima Bays, shell growth rate was generally low from January to April and then high during April to September. These data suggest that both reproduction and shell growth of this species are active from winter to early spring at Ariake Bay, but those occurred from late spring to summer at Tokyo and Kagoshima Bays.

Environmental Conditions of each Locality

Seasonal variations in water temperature, salinity, and content of chlorophyll *a* near the sampling localities are

shown in Figure 6. Seasonal changes in temperature and salinity are similar among them (Figure 6a, b). Also, spatial densities of individuals do not differ considerably among the habitats (Sato, personal observation). However, the seasonal cycle in phytoplankton abundance varies markedly among the bays. In Tokyo and Kagoshima Bays, the content of chlorophyll *a* increases in summer (June–August), but remains at low levels in the other seasons (Figure 6c). In contrast, in Ariake Bay, the content of chlorophyll *a* attains a maximum in winter (January–March) and is at low levels in the other seasons. The seasonal change of chlorophyll *a* usually reflects the phytoplankton abundance in each habitat, and generally the phytoplankton bloom occurs in spring in embayments of northern Japan, and in summer in those of central and southern Japan (Iizumi et al., 1990; Yamashita, 1982). The winter bloom in Ariake Bay is, therefore, a peculiar phenomenon for central and southern regions in Japan.

DISCUSSION

Genetic Control of Shell Growth Patterns

Both annual and seasonal shell growth patterns of the individuals transplanted from Tokyo, Ariake, and Kagoshima Bays to Aburatsubo Cove did not differ from those of the individuals in the original habitats (Figures 2, 3). These facts demonstrate that (at least for individuals of more than 2 years of age) transplanted individuals do not change their growth patterns in accordance with a new

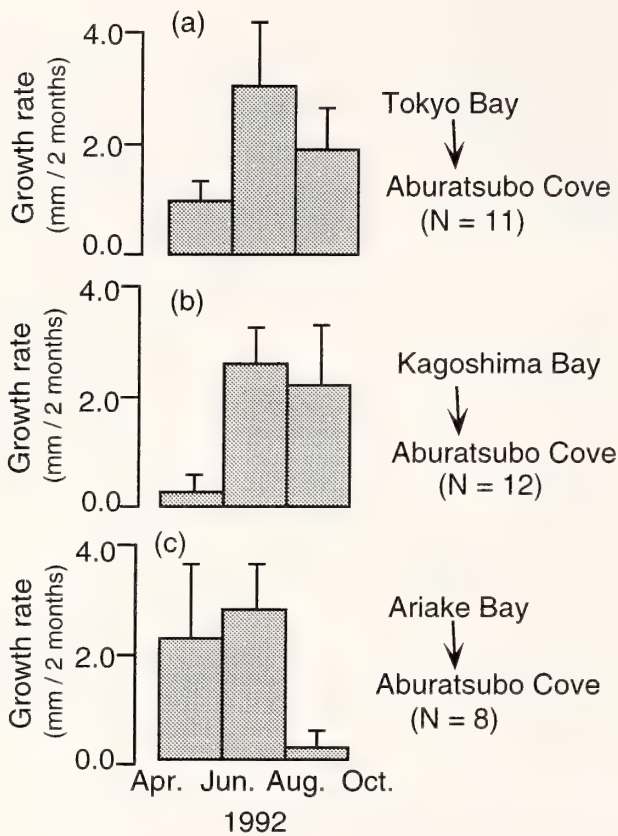


Figure 3

Mean bimonthly shell growth rate (April–June, June–August, August–October in 1992) among the 2 year old individuals transplanted from Tokyo Bay (a), Kagoshima Bay (b), and Ariake Bay (c) to Aburatsubo Cove. Mean and the range of one standard deviation (vertical bar) are indicated.

environment. The fact that the individuals from Ariake Bay could grow in Aburatsubo Cove as large as those in the original habitat, in spite of the stress expected for these transplanted animals, clearly indicates that the mode of shell growth in this species is not controlled directly by environmental factors.

Study of the genetic structure of this species showed that the genetic distance between the Tokyo and Ariake populations is nearly zero ($\hat{D} < 0.0005$), indicating a high gene flow between them (Sato, 1996). Nevertheless, the shell growth pattern and the age of sexual maturity differ markedly between them (Sato, 1994). These lines of evidence strongly suggest that shell growth and sexual maturity patterns of this species show phenotype plasticity against environmental fluctuations (Stearns, 1989). Available data taken from the transplant experiments in the present study, however, could not account for the existence of such phenotype plasticity in the shell growth patterns of this species. As a result, two possible alternative explanations for the genetic control of the shell

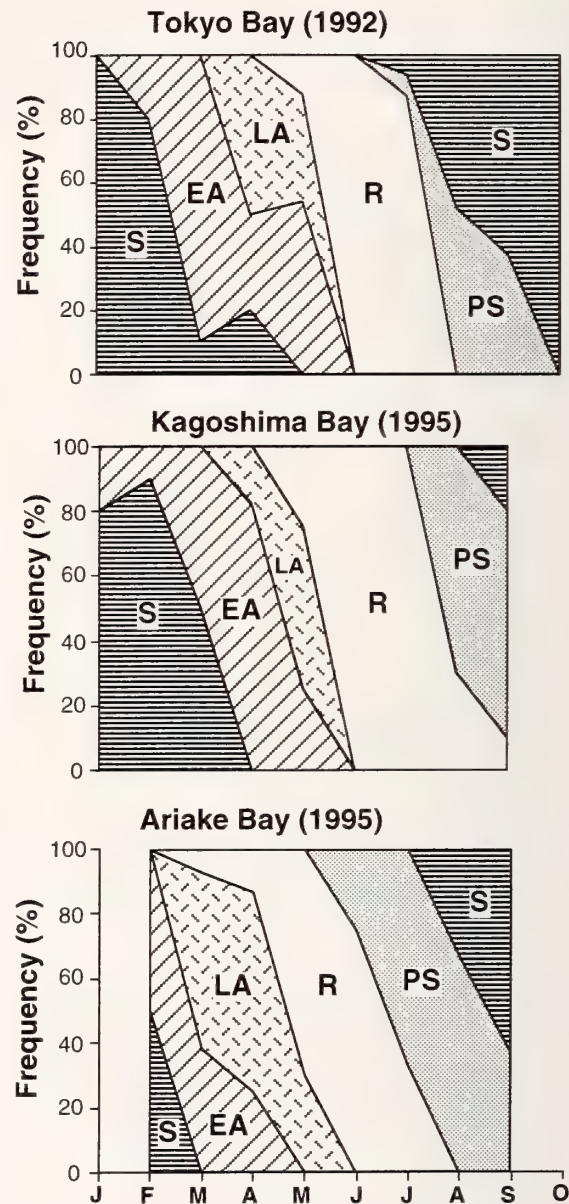


Figure 4

Frequency of occurrence of each phase of the reproductive cycle in monthly collected samples of *Phacosoma japonicum* from Kagoshima and Ariake Bays during January–September, 1995. Data from Tokyo Bay during January–October, 1992 from Sato (1995). (EA) early active phase, (LA) late active phase, (R) ripe phase, (PS) partially spawned phase, and (S) spent phase.

growth patterns are suggested: (1) phenotype plasticity may function when the individuals are younger than 2 years old, and (2) rapid evolution of the life-history traits may occur within several generations, which is too short to cause the differentiation in allozyme loci among populations. In order to clarify this question further transplant

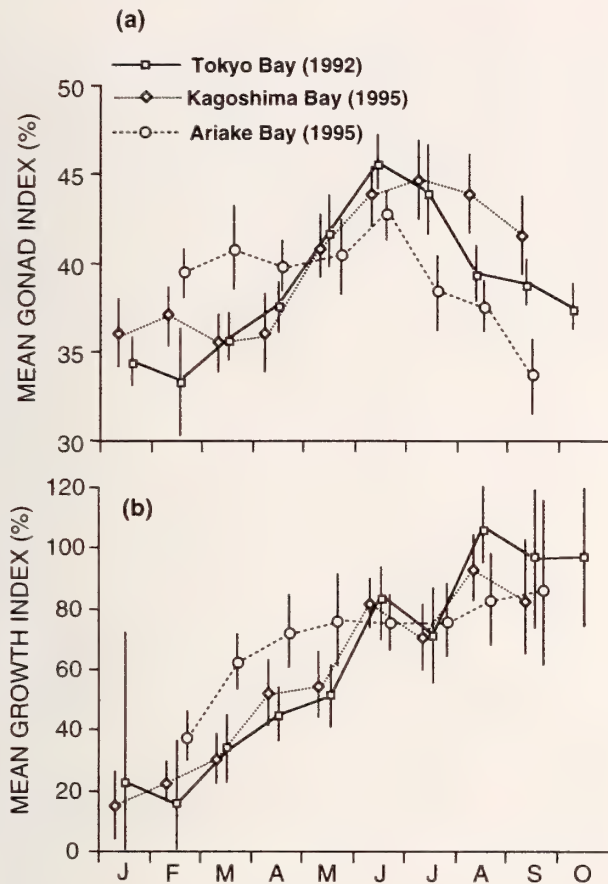


Figure 5

Seasonal changes in development of gonads (a) and shell growth (b) in mature specimens (> 4 years old) of *Phacosoma japonicum* from Kagoshima and Ariake Bays during January–September, 1995. Data from Tokyo Bay during January–October, 1992 from Sato (1995). Mean value and the range of one standard deviation (vertical bar) are indicated.

studies focusing on the juveniles of this species need to be done.

Relation of Life-History Traits to Environmental Factors

The growing seasons for both shell growth and gonad development in *Phacosoma japonicum* are limited to the interval between winter and early spring in Ariake Bay, and between late spring and summer in Tokyo and Kagoshima Bays (Figures 4, 5). Moreover, based on a sclerochronological study of the marked and recovered specimens, Tanabe (1988) detected rapid shell growth between April and September in the population of the Seto Inland Sea (southern Japan, see Figure 1). Tanabe & Oba (1988) also estimated the range of temperatures during the growing season from oxygen isotopic analysis of a specimen from Wakkanai Port, Hokkaido (northern Ja-

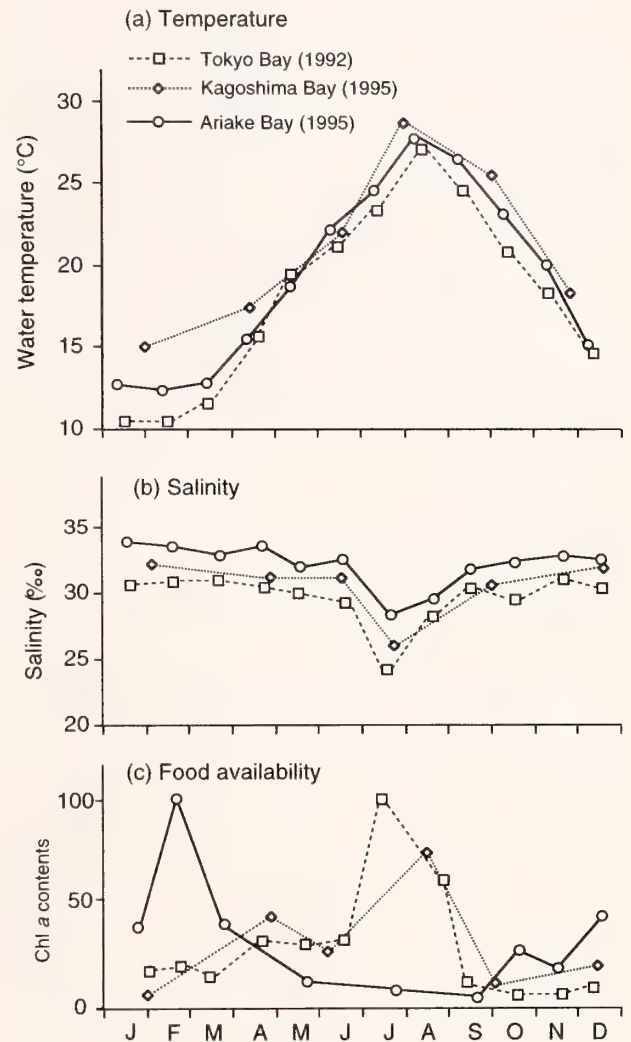


Figure 6

Monthly mean water temperature (a), salinity (b), and seasonal variations of chlorophyll *a* (c) near the sampling localities. Data sources are unpublished data of the Tokyo Metropolitan Office (Tokyo Bay in 1992), of the Kagoshima Environmental Research and Service (Kagoshima Bay in 1995), and of the Kumamoto Prefectural Fisheries Research Station (Ariake Bay in 1995).

pan, see Figure 1), and suggested that shell growth of the individual occurred between May and August. This difference in growing season between the Ariake and other populations is more plausibly explained by the difference in seasonal change of phytoplankton abundance than by factors such as temperature, salinity, and individual density. These data suggest that seasonal variations in shell growth and reproductive cycle of this species are primarily influenced by the seasonal change of food availability.

In this species, northern populations generally display more delayed sexual maturity and attain larger shell size at a given age than do southern ones (Figure 1). This

north-south gradient of life-history traits suggests that the difference in water temperatures among sampling sites is one of the factors which affects life-history traits in this species. Sebens (1979, 1987) introduced a model for optimum size at sexual maturation. According to him, the energy available for growth and reproduction is determined by the difference between energy intake and metabolic cost. The energy intake is primarily affected by food availability, and the metabolic cost in most poikilotherms is closely related to temperature (Sebens, 1979, 1980; Clarke, 1987). Because animals mostly utilize the energy during growing season for their growth and reproduction, the optimum size for sexual maturation for each population is determined by the food availability and water temperature during growing season.

In *Phacosoma japonicum*, both shell and gonad growth are generally limited to the interval between late spring and summer, except for the Ariake population. Because the phytoplankton bloom occurs in spring in northern Japan and in summer in central and southern Japan (Iizumi et al., 1990; Yamashita, 1982), energy intake during the growing season is sufficient. However, at lower latitude, the water temperatures during the growing season increase, so that metabolic cost during the growing season increases, and the optimum size for sexual maturation becomes smaller. This prediction from the optimum-size model is consistent with the north-south gradient of the life-history traits of *P. japonicum*.

Moreover, in the Ariake population, rapid shell growth and gonad development occurred in a limited period between February and April (Figures 4, 5). Since the phytoplankton productivity increases in winter in Ariake Bay, food resources during the growing season of *P. japonicum* are also sufficient. However, the mean water temperature during the growing season for the Ariake population (11–15°C: February–April) is much lower than those in neighboring regions (15–28°C: April–August) (Figure 6). Therefore, Sebens' model predicted that the optimum size at sexual maturation for the Ariake population is much larger than those in the neighboring regions, because more energy can be allocated to growth and reproduction due to the low metabolic rate in the growing season. This prediction agrees with the fact that shell size at sexual maturity of the Ariake population is much larger than those of the neighboring populations.

In conclusion, growing season in shell growth and reproduction of this species is strongly influenced by food availability, and the geographical variations of annual shell growth and sexual maturity patterns can be explained mainly by the mean water temperature during the growing seasons. Such intraspecific variations are genetically stable and are not influenced by short-term environmental changes.

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A Worldwide Review of the Food of Nudibranch Mollusks. Part II. The Suborder Dendronotacea

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Abstract. The prey items of 108 species representing all 10 families of the suborder Dendronotacea are presented in shortened form from the much larger electronic database accessible on the Web.

INTRODUCTION

This paper is the second paper in a series that will review the food of nudibranchs on a worldwide basis. As noted in the initial paper in this series (McDonald & Nybakken, 1997) these reviews are based on the published literature and are not the result of the investigations of the authors. Furthermore, each paper will be an abstracted version of a much larger database that contains all of the available information on the food of the nudibranchs extracted from an extensive search of the literature. This larger database has been deemed too large to publish in its entirety in hard copy and is available as the first electronic publication of the *The Veliger*. Electronic supplements and appendices of papers published in *The Veliger* are available via anonymous FTP from ucml1.Berkeley.Edu. These documents are available in three formats: PostScript (*.PS), Word-Perfect (*.WP), and ASCII (*.ASC). To retrieve a document, open an FTP connection to ucml1.Berkeley.Edu (128.32.146.30). At the request for login enter "anonymous." At the request for a password enter your e-mail address (e.g., jsmith@veliger.amu.edu). At the prompt change directory to /pub/mollusca/veliger (command = cd /pub/mollusca/veliger), set file transfer mode to binary (command = bin), and retrieve the desired file (command = get "filename.*"). At the end of your FTP session close the connection (command = close) and quit. The electronic files associated with this paper are nudifood1.ps, nudifood1.wp, and nudifood1.asc.

Introduction to the Dendronotacea

The suborder Dendronotacea is the second smallest in the order Nudibranchia. The number of living species worldwide is not precisely known due in part to the presence of several cryptic species of the speciose genus *Doto*

that have recently been uncovered through both molecular and morphological techniques (Morrow et al., 1992; Lemche, 1976; Goddard, 1996). This suggests that other single species in the genus may, in fact, be groups of cryptic species. We here report on the food of 108 species with representatives from all 10 families.

According to Thompson (1988) and Thompson & Brown (1984), this suborder is characterized by having the rhinophores retractile into sheaths, the dorsum margined with simple or branched processes and a mid-lateral anal opening. There has been no recent systematic review of the suborder since Odhner (1936).

RESULTS AND DISCUSSION

As can be seen from Table 1, the dendronotaceans have a somewhat varied diet, and the suborder includes both specialists and generalists. All species, however, prey on one or more species of the phylum Cnidaria. The species of the Tritoniidae all prey upon octocorals of the orders Alcyonacea, Gorgonacea, Pennatulacea, and Stolonifera (note in the table that if alcyonarians is listed it means that the order is not known and when alcyonaceans is used it means the order).

The families Lomanotidae, Embletoniidae, Hancockiidae, Bornellidae, Scyllaeidae, and Dotonidae all consume thecate and athecate hydroids. The Dendronotidae also seem to be primarily predators of thecate and athecate hydroids, but there are two species which appear to be specialists. They are *D. iris*, which feeds on cerianthid anemones, and *D. rufus*, which preys on scyphozoan scyphistomae.

The family Tethyidae all appear to feed primarily on small crustaceans which they capture using a large oral hood to sweep the organisms out of the water column or off the substrate.

Table 1
Summary of the food of the suborder dendronotacea.

Family	Genus	Species	Food
Tritoniidae	<i>Marionia</i>	<i>blainvillea</i>	on alcyonaceans (<i>Alcyonium</i>) and gorgonians (<i>Eunicella</i> , <i>Lophogorgia</i> , <i>Paramuricea</i>)
		<i>cucullata</i>	alcyonarians
		<i>occidentalis</i>	alcyonarians
	<i>Marioniopsis</i>	<i>quadrilatera</i>	alcyonaceans (<i>Alcyonium</i>)
		<i>cyanobranchiata</i>	alcyonaceans (<i>Xenia</i>)
		<i>platyctenea</i>	alcyonaceans (<i>Parerythropodium</i>)
	<i>Paratritonia</i>	<i>lutea</i>	gorgonians (<i>Mopsella</i>)
	<i>Tochuina</i>	<i>tetraquetra</i>	alcyonaceans (<i>Gersemia</i>), pennatulaceans (<i>Ptilosarcus</i>)
			on alcyonaceans (<i>Alcyonium</i>)
	<i>Tritonia</i>	<i>alba</i>	<i>Melitodes</i> gorgonians (<i>Briareum</i> , <i>Pseudopterogorgia</i>)
		<i>aurantiaca bayeri</i>	pennatulids (<i>Ptilosarcus</i> , <i>Stylatula</i> , <i>Virgularia</i>)
		<i>diomedea</i>	stoloniferans (<i>Clavularia</i>), alcyonaceans (<i>Gersemia</i>), gorgonians (<i>Lophogorgia</i>), and pennatulids (<i>Ptilosarcus</i>)
		<i>festiva</i>	gorgonian (<i>Paramuricea</i>)
		<i>griegi</i>	gorgonian (<i>Gorgonia</i>)
		<i>hammerorum</i>	stoloniferan (<i>Anthelia</i>)
		<i>hawaiiensis</i>	alcyonacean (<i>Alcyonium</i>)
		<i>hombergi</i>	alcyonarians (<i>Alcyonium</i>)
		<i>incerta</i>	stoloniferan (<i>Sarcodictyon</i>)
		<i>lineata</i>	stoloniferan (<i>Cornularia</i>)
		<i>manicata</i>	gorgonians (<i>Eunicella</i> , <i>Lophogorgia</i>)
		<i>nilsodhneri</i>	gorgonians (<i>Muricea</i> , <i>Psammogorgia</i>)
		<i>pickensi</i>	alcyonaceans (<i>Alcyonium</i>), gorgonians (<i>Eunicella</i> , <i>Lophogorgia</i> , <i>Paramuricea</i>)
		<i>plebeia</i>	alcyonacean (<i>Paralcyonium</i>)
		<i>striata</i>	stoloniferan (<i>Pachyclavularia</i>)
		<i>vorax</i>	gorgonians (<i>Gorgonia</i> , <i>Leptogorgia</i>)
		<i>wellsi</i>	stoloniferans (<i>Clavularia</i> , <i>Pachyclavularia</i>)
	<i>Tritoniella</i>	<i>belli</i>	"soft coral" on gorgonians
	<i>Tritoniopsis</i>	<i>alba frydis</i>	hydroids thecate hydroids (<i>Kirichenpaueria</i> , <i>Ventromma</i>)
Marianinidae	<i>Marianina</i>	<i>rosea barlettai</i>	thecate hydroids (<i>Antennularia</i> , <i>Nemertesia</i>)
Lomanotidae	<i>Lomanotus</i>	<i>flavidus</i>	on thecate hydroids (<i>Antennularia</i> , <i>Nemertesia</i>), athecate hydroids (<i>Tubularia</i>) and bryozoans (<i>Cellaria</i>)
		<i>genei</i>	thecate hydroids (<i>Antennularia</i> , <i>Nemertesia</i>)
		<i>marmoratus</i>	thecate hydroid (<i>Lytocarpus</i>)
		<i>vermiformis</i>	on thecate hydroid (<i>Obelia</i>)
		<i>evelinae</i>	campanularid hydroids
Embletoniidae	<i>Embletonia</i>	<i>gracilis</i>	thecate hydroids (<i>Antennularia</i> , <i>Nemertesia</i> , <i>Hydrallmania</i>); athecate hydroids (<i>Cordylophora</i> , <i>Tubularia</i>)
		<i>pulchra</i>	

Table 1
Continued.

Family	Genus	Species	Food
Hancockiidae	<i>Hancockia</i>	<i>uncinata</i>	thecate hydroids (<i>Campanularia</i> , <i>Clytia</i> , <i>Nemertesia</i> , <i>Obelia</i>); athecate hydroids (<i>Tubularia</i>)
Dendronotidae	<i>Dendronotus</i>	<i>albopunctatus</i> <i>albus</i>	on athecate hydroids (<i>Tubularia</i>) thecate hydroids (<i>Abietinaria</i> , <i>Plumularia</i> , <i>Thuiaria</i>); athe- cate hydroid (<i>Tubularia</i>)
		<i>dalli</i>	thecate hydroid (<i>Abietinaria</i>)
		<i>diversicolor</i>	thecate hydroids (<i>Abietinaria</i> , <i>Hydrallmania</i> , <i>Sertularella</i>)
		<i>frondosus</i>	thecate hydroids (12 genera); athecate hydroids (7 genera); ascidiacean (<i>Botryllus</i>)
		<i>iris</i>	cerianthid anthozoans (<i>Pachycer- iathus</i>); thecate hydroids (<i>Obelia</i>)
		<i>robustus</i>	beetles!; campanularid hydroids; oweniid polychaetes
		<i>rufus</i>	scyphozoan schyphistomae
		<i>subramosus</i>	thecate hydroids (<i>Aglaophenia</i> , <i>Obelia</i>); athecate hydroid (<i>Tubularia</i>)
Bornellidae	<i>Bornella</i>	<i>stellifer</i>	thecate hydroid (<i>Sertularia</i>)
Scyllaeidae	<i>Crosslandia</i>	<i>anguilla</i>	thecate hydroid (<i>Plumularia</i>)
	<i>Notobryon</i>	<i>daedali</i>	hydroids
Tethyidae	<i>Scyllaea</i>	<i>wardi</i>	campanularid hydroids
	<i>Melibe</i>	<i>pelagica</i>	hydroids
		<i>bucephala</i>	detritus and microorganisms on algae
		<i>fimbriata</i>	crustaceans
		<i>leonina</i>	amphipods, bivalve spat, cope- pods, isopods, ostracods, small crustaceans, veliger larvae, zoea larvae, megalops larvae
		<i>megaceras</i>	small crustaceans
		<i>mirifica</i>	small crustaceans
		<i>pilosa</i>	copepods, isopods, portunid crab, small crustacea
		<i>rosea</i>	amphipods
	<i>Tethys</i>	<i>fimbria</i>	amphipods, ophiuroids (<i>Amphi- ura</i> , <i>Ophioglypha</i>), copepods, crustaceans, brachyurans, iso- pods, ostracods, small echino- derms, small gastropods, sto- matopods, worms
Dotonidae	<i>Doto</i>	<i>acuta</i>	thecate hydroid (<i>Obelia</i>)
		<i>amyra</i>	thecate hydroids (<i>Abietinaria</i> , <i>Aglaophenia</i> , <i>Bougainvillia</i> , <i>Obelia</i> , <i>Sertularia</i>)
		<i>arteoi</i>	thecate hydroid (<i>Laomedea</i>)
		<i>aurita</i>	on athecate hydroid (<i>Tubularia</i>)
		<i>chica</i>	on athecate hydroid (<i>Euden- drium</i>)
		<i>cindyneutes</i>	on thecate hydroid (<i>Halecium</i>)
		<i>cinerea</i>	on thecate hydroids (<i>Aglaophen- ia</i> , <i>Sertularia</i>)

Table 1
Continued.

Family	Genus	Species	Food
		<i>columbiana</i>	on thecate hydroids (<i>Aglaophenia</i> , <i>Obelia</i> , <i>Selaginopsis</i>) and on athecate hydroids (<i>Tubularia</i>)
		<i>coronata</i>	16 genera of thecate hydroids and 10 genera of athecate hydroids and the bryozoan <i>Alcyonidium</i>
		<i>cuspidata</i>	thecate hydroids (<i>Nemertesia</i>)
		<i>doerga</i>	thecate hydroids (<i>Aglaophenia</i> , <i>Obelia</i>)
		<i>dunnei</i>	thecate hydroid (<i>Kirchenpaueria</i>)
		<i>eireana</i>	thecate hydroids (<i>Dynamena</i> , <i>Sertularia</i>)
		<i>floridicola</i>	on thecate hydroids (<i>Aglaophenia</i> , <i>Synthecium</i>)
		<i>formosa</i>	athecate hydroid (<i>Eudendrium</i>)
		<i>fragilis</i>	thecate hydroids (<i>Antennularia</i> , <i>Halecium</i> , <i>Hydrallmania</i> , <i>Nemertesia</i>) and athecate hydroids (<i>Tubularia</i>)
		<i>furva</i>	on thecate hydroids (<i>Campanularia</i> , <i>Filellum</i> , <i>Halecium</i> , <i>Sertularia</i> , <i>Sertularella</i>)
		<i>ganda</i>	on thecate hydroid (<i>Obelia</i>)
		<i>hydrallmaniae</i>	thecate hydroid (<i>Hydrallmania</i>)
		<i>hystrix</i>	thecate hydroid (<i>Schizotricha</i>)
		<i>japonica</i>	on thecate hydroid (<i>Aglaophenia</i>)
		<i>koenneckeri</i>	thecate hydroid (<i>Aglaophenia</i>)
		<i>kya</i>	thecate hydroids (<i>Abietinaria</i> , <i>Aglaophenia</i> , <i>Obelia</i> , <i>Plumularia</i> , <i>Sertularella</i> , <i>Sarsia</i>) and athecate hydroids (<i>Eudendrium</i>)
		<i>lancei</i>	thecate hydroids (<i>Aglaophenia</i>)
		<i>lemchei</i>	thecate hydroids (<i>Aglaophenia</i> , <i>Synthecium</i>)
		<i>maculata</i>	thecate hydroids (<i>Halopteris</i> , <i>Plumularia</i> , <i>Schizotricha</i>)
		<i>millbayana</i>	thecate hydroids (<i>Aglaophenia</i> , <i>Nemertesia</i> , <i>Plumularia</i>)
		<i>oblicua</i>	thecate hydroids (<i>Amphisbetia</i> , <i>Sertularia</i>)
		<i>onusta</i>	thecate hydroid (<i>Dynamena</i>)
		<i>paulinae</i>	thecate hydroids (<i>Aglaophenia</i> , <i>Obelia</i>) and athecate hydroid (<i>Eudendrium</i>)
		<i>pinnatifida</i>	thecate hydroids (<i>Aglaophenia</i> , <i>Antennularia</i> , <i>Halecium</i> , <i>Nemertesia</i> , <i>Obelia</i> , <i>Sertularia</i>)
		<i>pita</i>	on thecate hydroids (<i>Clytia</i> , <i>Obelia</i> , <i>Sertularella</i> , <i>Orthopyxis</i>)
		<i>pontica</i>	on thecate hydroid (<i>Aglaophenia</i>)
		<i>rosea</i>	on athecate hydroid (<i>Eudendrium</i>)
		<i>sarsiae</i>	athecate hydroid (<i>Sarsia</i>)

Table 1
Continued.

Family	Genus	Species	Food
Phylliroidea	<i>Phyllirhoe</i>	<i>tuberculata</i>	thecate hydroids (<i>Abietinaria</i> , <i>Sertularella</i>)
		<i>unguis</i>	thecate hydroid (<i>Nemertesia</i>)
		<i>ussi</i>	on thecate hydroid (<i>Aglaophenia</i>)
		<i>uva</i>	on thecate hydroid (<i>Pennaria</i>)
		<i>verdicioi</i>	thecate hydroids (<i>Aglaophenia</i> , <i>Laomedea</i>)
		<i>wara</i>	on thecate hydroid (<i>Aglaophenia</i>)
	<i>Cephalopyge</i>	<i>bucephala</i>	thecate hydroid medusae (<i>Aequorea</i>); athecate hydroid medusae (<i>Zanclus</i>); larvaceans (<i>Oikopleura</i>)
		<i>mediterranea</i> <i>trematoides</i>	siphonophores (<i>Halistemma</i>) siphonophores (<i>Nanomia</i> , <i>Halistemma</i> , <i>Stephanomia</i>)

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The Giant Amazonian Snail (Pulmonata: Acavidae) Beats Them All

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Abstract. *Pebasiconcha immanis* gen. & sp. nov. is described from the Miocene Pebas Formation of Colombian Amazonia. Apart from a simple outer lip of the aperture and a prominent external “mytiloid” thickening shortly below the suture, behind the lip, the genus resembles *Strophocheilus*. It is the largest terrestrial gastropod now known to have ever existed, and one of only two species of terrestrial snails recorded from the Pebas Formation. Its shells are approx. 20% higher than those of the largest Achatinidae known.

INTRODUCTION

Species of the Achatinidae are generally considered the largest terrestrial snails that ever lived on earth. That gastropod family, including the Giant African Snails of popular writing, is restricted to tropical Africa. Their fusiform shells may reach approx. 21 cm in height. South American species of the Acavidae, Strophocheilinae, have long been second on the world list, with similar shells up to 16 cm high.

During fieldwork in deposits of the Miocene Pebas Formation in Colombian Amazonia, in the autumn of 1991, some remarkably large shells of snails were found. These shells, locally common in the formation, were initially classified with the genus *Strophocheilus* Spix, 1827 (Pulmonata: Acavidae: Strophocheilinae); later, it was observed that they differ in apertural characters, however. The working conditions did not permit the transport of complete shells (that were broken into pieces and disintegrated), but photographs were made of an entire specimen *in situ*. A second visit to the area in 1996 yielded only additional shell fragments. On this visit, however, in a shop in Iquitos, Peru, though not for sale, a single well-preserved specimen was discovered; this shell could also be photographed. Therefore, the current description of a new genus and species is based on photographs and shell fragments.

The species is one of only two terrestrial pulmonate species recorded from the Miocene Pebas Formation, which is rich in fresh- and brackish-water mollusks. It is truly giant in size. The maximal height of the fusiform shell, directly observed, is 25.6 cm; on the basis of shell fragments, similar dimensions can be calculated. This dis-

covery implies a 20% increase in the maximum shell size known for terrestrial snails, dethroning the Giant African Snails in favor of this “Giant Amazonian Snail.”

SYSTEMATIC PALEONTOLOGY

Class Gastropoda

Order Stylommatophora A. Schmidt, 1855

Family ACAVIDAE Pilsbry, 1895

Subfamily STROPHOCHEILINAE Thiele, 1926

Pebasiconcha immanis Wesselingh & Gittenberger gen. & sp. nov.

(Figures 1, 2)

Holotype (Figure 1a): a shell, complete when collected but secondarily broken into pieces (Instituto de Investigaciones en Geociencias, Minería y Química [“Ingeominas”], Bogotá, Colombia, unnumbered).

Paratypes: Nineteen shell fragments from the type locality and type stratum (Figure 2a, b) (Nationaal Natuurhistorisch Museum, Leiden, The Netherlands - RGM 394327/30); a complete shell from locality 2 (Figure 1b,c) (M. Callegari, private collection, Iquitos, Peru).

Type locality and locality 2: The holotype was found September 1991 by the first author in Colombia, State of Amazonas, in the cliff at the northern side of the confluence of the rivers Amazonas and Loreto-Yacu, 1 m above the water table. The locus typicus is in the Pebas Formation, and is assigned to a late Middle to early Late Miocene age (*Grimsdalea* zone) (Hoorn, 1994). Locality



Figure 1

Pebasiconcha immanis Wesselingh & Gittenberger gen. & sp. nov. a. holotype [height 25.6 cm] (irreparably broken after the photograph had been taken in the field), with the "mytiloid" knob indicated by an arrow ("Ingeominas" Collection, Bogotá, Colombia, unnumbered). b–c. paratype [height 21.9 cm] from the vicinity of Pebas, Loreto department, Peru (M. Callegari private collection, Iquitos, Peru, unnumbered). Photos: F. Wesselingh.

2 cannot be indicated more exactly than "vicinity of" Pebas, Loreto department, Peru; outcrops from that area have been assigned to a Middle Miocene age (*Crassoretiriletus* zone) (Hoorn, 1994).

Diagnosis: Shell very large, reaching over 25 cm in height; body whorl with a markedly constricted aperture; apertural lip neither thickened nor reflected; upper half of the body whorl, shortly behind the apertural lip, with a conspicuous knob, accompanied more posteriorly by a less prominent swelling.

Description: The ovoid shell has up to nearly six moderately convex whorls, separated by a suture, which becomes more strongly indented toward the aperture. The body whorl measures approx. four-fifths of and the aperture approx. one-third of the total shell height; it is slightly more flattened than the preceding whorls. The protoconch sculpture is unknown because the initial whorls are abraded or dissolved in all specimens. The teleoconch has irregular prosocline riblets that are most prominent at the apical side of the whorls. The penultimate whorl has about 170 such riblets. In between them,

small malleated areas may occur, in particular on fragments with a weakly developed sculpture. On most of the body whorl the riblets are more or less obsolete, and the surface is somewhat malleated. There is a prominent, asymmetrical knob (Figures 1a, 2b) on the upper half of the body whorl, shortly behind the apertural border. This knob has a well-defined, narrow tip shortly below the suture and a broadly rounded basal part; in curvature it is reminiscent of a *Mytilus* valve. Toward the back, there is a far more obsolete roundish knob. The final quarter of the body whorl has a concave shoulder which is increasingly more prominent toward the aperture (Figure 1c). The aperture is markedly constricted. Its outer lip is regularly curved and nearly circular, with the border neither reflected nor thickened. The inner lip is straightened, with a relatively thin parieto-columellar callus. The umbilicus is closed or slitlike; in some specimens a damaged, very narrow columellar canal is visible.

Several fragments and the complete paratype bear irregularly arranged low ridges on the ultimate and the penultimate whorls. On the lower half of the whorls these ridges are spirally arranged, whereas on the upper half



Figure 2

Pebasiconcha immanis Wesselingh & Gittenberger, gen. & sp. nov., paratypes from the type locality & type stratum.
a. apical fragment, RGM 394328. b. upper palatal wall fragment, with the "mytiloid knob," RGM 394329. G. A. Peeters del.

they converge obliquely toward the periphery. Some fragments have a brownish layer, possibly a remnant of the periostracum.

Dimensions: The holotype suffered severely from transport. Because it had been photographed before, however, its size could be calculated as approx. 25.6 cm high and 14.5 cm broad; the aperture, measured outside, in frontal view, is 8.7 cm high and 8.2 cm broad. The locality 2 paratype measures 21.9×11.8 cm; its aperture is 7.0 cm high and equally broad. An apical fragment (RGM 394328; Figure 2a) is similar to the holotype in size. A fragment of the palatal apertural wall, with the “mytiloid” knob included (Figure 2b), is either of a specimen higher than 30 cm, or of a shell with a relatively large knob as compared to the holotype.

Recently, Dr. A. J. de Winter (Nationaal Natuurhistorisch Museum, Leiden) bought a shell of *Archachatina marginata* (Swainson, 1821), measuring 21.3×12.4 cm, from a villager at Nyangong, SW. Cameroun (De Winter, 1997). According to Dr. A. Mead (1961, and in litt., 24 April 1995), this specimen is larger than any shells of Giant African Snails recorded in his personal database; the shell is slightly aberrant in shape, however, which might be indicative of abnormal growth. A single shell of *Achatina achatina* (Linnaeus, 1758) is reported by Parkinson et al. (1987:33), as “one exceptional specimen” of 27.3 cm, of this well-known species, normally measuring “up to 20 cm” only. Because of the magnitude of the difference in size with specimens hitherto reported, we prefer to consider this specimen an aberration, not to be considered in the regular species description. The “Giant Amazonian Snail,” known from far fewer specimens, is considerably larger than the Giant African Snails.

Classification and differentiation: The assignment of this species to the Acavidae, Strophocheilinae, is based on the size, shape, and sculpture of the shell, in particular the prosocline riblets at the apical side of the whorls, and its occurrence in Amazonia. Without anatomical data, this assignment has to remain poorly based. The closest relatives of this species might also be found among the Bulimulidae or the Orthalicidae, mainly differing conchologically by somewhat lower maxima in shell size (Zilch, 1960).

The genus *Strophocheilus* Spix, 1827, is known from the neotropical region only, from the Paleocene on (Parodiz, 1969; Zilch, 1960). *Pebasiconcha immanis* differs from all *Strophocheilus* species by its very large size and particularly by the simple outer lip of the aperture and the “mytiloid” knob on the body whorl, shortly behind the lip. In *Strophocheilus* the straight outer lip is always clearly thickened, a generic autapomorphy, and the surface of the body whorl is not provided with any knobs. The simple outer lip in *Pebasiconcha*, found in many gastropod shells, may be considered a plesiomorphous

character state (if not a reversal), whereas giant size and “mytiloid” knob are seen as autapomorphies.

Habitat: The Pebas Formation has been deposited in a fluvio-lacustrine to permanently lacustrine palaeo-environment (Hoorn, 1994). The deposits are rich in aquatic mollusks, i.e., cochliopine hydrobiids and pachydontine corbulids. Forty-four species are now known from these deposits (Nuttall, 1990). Despite predominantly lacustrine conditions in western Amazonia during the Middle Miocene, swamplike conditions and forested riverbanks must also have been present (Hoorn, 1994). Therefore, the number of only two terrestrial gastropod species, both pulmonates, *P. immanis* and *Orthalicus linteus* (Conrad, 1871) is remarkably low. The latter species probably lived on tree trunks and branches, the habitat occupied by the many congeneric Recent species. *Pebasiconcha immanis* might have lived on the humid bottom, where gravity is less problematic; it seems unlikely that such huge snails would have climbed trees.

In outcrops of the Pebas Formation, concentrates of severely damaged specimens and fragments of *P. immanis* are common. Smaller, more clearly abraded fragments can be found dispersed throughout the deposits. The concentrates are often part of lignitic lags. At the type locality there are two such lags, overlain there by incursion layers containing abundant mangrove pollen, foraminifera, and marine gastropods. The poor internal sorting of these lags and the preservation of delicate structures on some of the shell fragments (RGM 394327) indicate a rapid deposition without much reworking, suggesting marine incursions in a fluvio-lacustrine environment. For other lags with concentrates of *P. immanis* no relation with incursion events is seen.

Etymology: Generic name after the Pebas Formation and *concha*, Latin for shell. Epithet *immanis*, Latin for enormous, huge, etc.

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Gastropods and Intertidal Soft-Sediments: The Case of *Chilina ovalis* Sowerby (Pulmonata: Basommatophora) in South-Central Chile

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Abstract. Field experiments (exclusion and inclusion of gastropods) were carried out in the intertidal of the Lingue River estuary (south-central Chile) during the summers of 1991 and 1992. Cages were used to analyze the effects of the snail *Chilina ovalis* Sowerby on the macroinfaunal community structure and the sedimentological properties of the top (1.5 cm) layer of the substrate. The experiments lasted 30 (1991) and 90 days (1992). We also studied the quality of sediment in snail trails versus sediment without trails, and the abundance and size structure of *C. ovalis* over a period of 15 months. In both field experiments, *C. ovalis* affected neither the macroinfaunal structure nor the sediment quality. Significant differences were detected for chlorophyll *a* content (phytobenthic biomass) when disturbed (trails sediment) versus undisturbed sediment were compared. The highest abundance of *C. ovalis* (up to 792 ind/m⁻²) occurred during summer months when the experiments were carried out. It is concluded that the disturbance of intertidal sediment by *C. ovalis* is quite local and of short duration, a situation which is discussed in connection with physical and biological factors involved in sediment stability and community organization of macroinfaunal assemblages.

INTRODUCTION

Epibenthic organisms such as decapod crustaceans and gastropod mollusks can play key roles in structuring the sediment and the macroinfauna of soft bottom substrates (Dayton, 1984; Wilson, 1990; Hall et al., 1993). Biological disturbance can alter the fabric and stability of the sediment (Brenchley, 1981; Posey, 1987) and affect the food availability by depletion of phytobenthic biomass (Connor et al., 1982). Epibenthos can also ingest macroinfaunal larvae or adults (Möller, 1986; Hines et al., 1990), bury and kill post-settlement infauna, or induce escape behavior (Ambrose, 1984; DeWitt & Levinton, 1985; Jensen & Jensen, 1985).

Manipulative experiments carried out with prosobranch gastropods have shown effects of these organisms on various components of the benthos (see Lopez & Levinton, 1987). Levinton & Stewart (1982) documented negative effects of *Ilyanassa obsoleta* Say and *Hydrobia totteni* Morrison on the population growth of the oligochaete *Paranais litoralis* Müller. The same gastropod species affected biomass and metabolism of benthic diatoms (Levinton & Bianchi, 1981; Connor et al., 1982), and the standing stock of bacteria adhering to the sediment (Bianchi & Levinton, 1981). In salt marsh areas of eastern England, Frid & James (1988) found an increase in the abundance of oligochaetes and the polychaete *Capitella capitata* Fauvel, resulting from removal of the epibenthic gastropod *Littorina littorea* (L.). In muddy salt marsh areas of Georgia (USA), Pace et al. (1979) found that the effects of *I. obsoleta* were related more to the ingestion of microorganisms than mechanical changes produced in

the substrate. This snail species significantly affected the abundance of recently settled and juvenile meiofauna and macroinfauna in tidal flats of North Carolina, USA (Hunt et al., 1987). Similar results were reported by Wiltse (1980) who studied the effects of the snail *Polinices duplicatus* (Say) on the tidal flats of Barnstable Harbor, USA.

Knowledge of the ecology of epibenthic gastropods on other coasts is rather scarce. In estuarine areas of south central Chile (ca. 38–40° S), the endemic pulmonate gastropod *Chilina ovalis* Sowerby, 1842, resembles *Ilyanassa obsoleta*, in spite of geographical and phylogenetic differences (Brown & Pullan, 1987; Castellanos & Miquel, 1991). *Chilina ovalis* gathers in muddy areas with high nutrient content, i.e., organic matter, and its movement and surface deposit-feeding habits produce noticeable changes in the substrate (trails). Deposit feeding in *C. ovalis* could be a secondary feeding mode, considering that other species of the genus have been described as periphyton consumers above hard substrates (Miquel, 1986; Bosnia et al., 1990).

In the Queule and Lingue River estuaries, *C. ovalis* coexists with polychaetes and amphipods (Richter, 1985; Bertrán, 1989; Quijón & Jaramillo, 1993; Quijón et al., 1996). Seasonal studies carried out on the subtidal populations of such taxa show that their main periods of recruitment occur during the spring-summer months (Bravo, 1989; Quijón et al., 1996). Our unpublished data show similar trends for intertidal populations. Feeding trails of *C. ovalis* alter the surface layer of the sediment to an approximate depth of 0.5 cm where the highest abundance of adults and recruits of the macroinfauna are

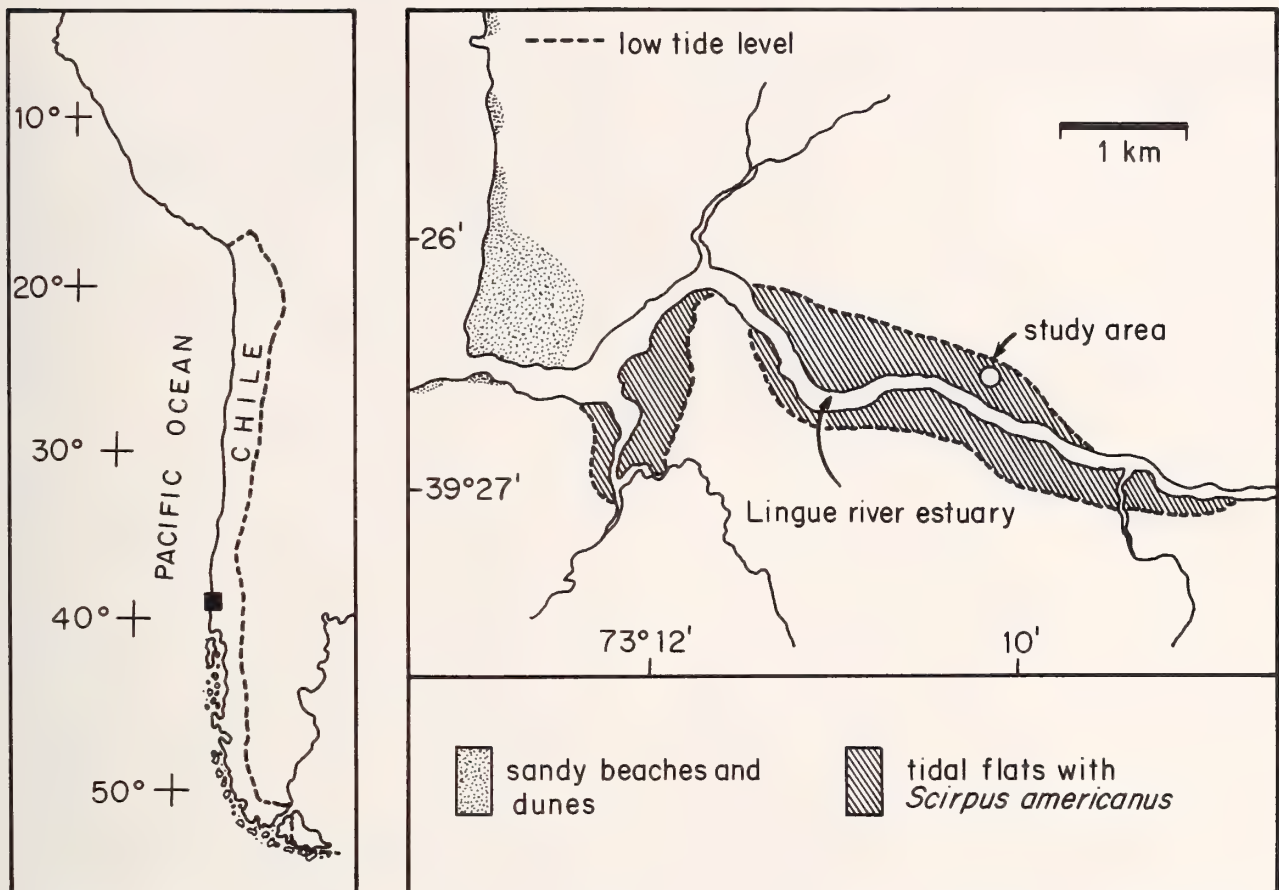


Figure 1

Study area in the Lingue River estuary, south-central Chile.

concentrated (unpublished data). We hypothesize that *C. ovalis* affects the sediment and community structure of the macroinfauna on the intertidal estuarine sediment of southern Chile. In order to test this hypothesis, the abundance of *C. ovalis* was experimentally manipulated in the intertidal zone of the Lingue River estuary during the summers of 1991 and 1992. In addition, analyses of sediment with and without trails of gastropods, as well as gastropod population analyses, were carried out.

MATERIALS AND METHODS

Study site: Figure 1 shows the middle section of the Lingue River estuary, in south-central Chile (39°41'S, 73°13'W). Upper shore levels of tidal flats are occupied by sedges *Scirpus americanus* Pers; close to them, the largest aggregations of *C. ovalis* have been observed. Sedges occur in association with muddy-sand substrates rich in organic content (ca. 20% of dry weight); their stems are used by the snails to deposit their egg masses (cf. Miquel, 1984).

Abundance and population size structure of *C. ovalis*:

The abundance of *C. ovalis* and the body size structure of the population were characterized by using 25 cm × 25 cm quadrats on a monthly sampling schedule. The samples (six replicates) were collected in sediments with a representative range of *S. americanus* canopy. The abundance and overall shell length, i.e., body size of the individuals were used to estimate the size structure of the population. The Battacharya's method (Gayanilo et al., 1989) was used for identification of modes, i.e., cohorts in the size-class distribution of *C. ovalis*. "Modal Progress Analysis" (MPA); a section of the "ELEFAN" program was used for the analysis of temporal variability of modes (Gayanilo et al., 1989).

Field experiments: The experimental design consisted of the following treatments: inclusion (natural densities) and exclusion cages of snails, undisturbed sediments (control), and partial walls as a control for possible artifact effects produced by the cages (Reise, 1985; Hall et al., 1990). To detect eventual cage artifact effects, sediments

of control and wall treatments were compared. The inclusion and exclusion cages were made with circular meshes of galvanized steel of 1 mm aperture, 30 cm diameter, and 10 cm height, buried to a depth of 3 cm in the substrate. Partial cages were made with similar materials and dimensions, but 50% of the perimeter was open to allow free movement of the snails.

The experiments were carried out for 30 days during the summer of 1991 (four replicates for each treatment, starting date: January 5) and for 90 days during the summer of 1992 (six replicates for each treatment, starting date: November 4, 1991). All the treatments (replicated cages and unmanipulated sites) were located on areas of the flat adjacent to *S. americanus* fronds. The cages, i.e., replicates in the sense of Hurlbert (1984) were randomly placed at an average distance of 40 m from low tide level. Independent sediment samples were collected for analysis of texture, water, organic matter, and chlorophyll *a* contents and macroinfauna. Three samples were collected from each one of the replicates of each treatment with plastic cylinders 1 cm in diameter. Samples were collected during the low tides of days indicated in Figures 3–6.

Sediment comparisons: A sediment comparative study was conducted during a spring low tide of November 1993. Sediment from freshly produced feeding trails of *C. ovalis* and from adjacent undisturbed areas was sampled and compared. Twenty “sets” of samples with similar volumes were collected with a metallic spatula inserted to a depth of 0.5 cm in the substrate. Independent sediment samples were used for analyses of texture, water, organic matter, and chlorophyll *a* contents.

Samples and data analysis: Sedimentological analyses were carried out as follows: sand and biogenic aggregates, i.e., animal feces, tubes (both in the range 63–2000 μm) were separated from the mud fraction (particles < 63 μm) by wet sieving through a 62.5 μ sieve (Anderson et al., 1981). Later, sand and aggregates were separated by wet sieving through a 62.5 μ sieve after disaggregation through sonification for 30 min. The water and organic matter contents of independent sediment samples were determined as the loss in weight of wet samples after drying (80°C, 72 h) and after combustion (550°C, 4 h). Sediment samples for chlorophyll *a* content analysis (used here as an estimate of phytobenthic biomass) were kept in 90% acetone for 24 h to extract pigments; then they were centrifuged at 3500 rpm for 15 min. The absorbance of the supernatant was measured at 750 and 665 nm with and without acidification by HCl 0.1 N (Strickland & Parsons, 1972). The samples for the faunistic analyses were sieved with a 0.25 mm mesh and the residue was preserved in formaldehyde 10% until sorting.

The sedimentological and faunistic (abundance and species-richness) characteristics were used for statistical comparisons among treatments in the field experiments. In addition, sedimentological characteristics were used

for statistical comparisons between sediments with and without trails.

One-way analyses of variance (Sokal & Rohlf, 1969) were used except when the values were not normally distributed. In these cases, a non-parametric analysis (Kruskal-Wallis ANOVA) was used. Percentage data were transformed by the expression $\arcsin(n)$ and the abundance values by $\log_{10}(n + 1)$ (Sokal & Rohlf, 1969). If the analyses of variance indicated significant differences ($p < 0.05$) among means, these were compared using the a posteriori Tukey's multiple comparison test (Day & Quinn, 1989).

RESULTS

Abundance and population size structure of *C. ovalis*:

The highest abundance of *C. ovalis* (up to 792 ind/m²) and number of trails were observed during the summer months (after the start of the snail recruitment period). The population abundance declined to 0 ind/m² during the winter of 1992 (July–August). Then the population increased after September of that year (Figure 2; no samples were collected during November). Comparison of abundance during December and January of both years indicated interannual variations.

Table 1 shows the average size of the cohorts and the monthly increase in these averages (months with $N < 50$ were not included in the analyses). The largest mean size increases of the 1990 and 1991 cohorts (1.335 and 2.251 mm/month, respectively) were observed during summer months (February–March 1992).

Field experiments: Most of the statistical comparisons (one way ANOVA) carried out with the data of the field experiments showed no significant differences ($p > 0.05$) among treatments (Tables 2, 3 and Figures 3–6).

The results of analyses with sedimentological characteristics (Table 4) showed F values between 0.05 and 2.58 during the experiment carried out in 1991, and between 0.02 and 5.58 during 1992. The *P* values fluctuated between 0.101 and 0.984 in 1991, and between 0.006 and 0.996 in 1992. Thus, only during the second experimental period were significant differences among the treatments detected (Figure 4): the sand content of the control treatment was significantly higher than those estimated for inclusion and exclusion sediments (day 8, $P = 0.006$); and the sand content of the control sediments was higher than that estimated for inclusion treatment (day 90, $P = 0.037$).

When the abundance and species-richness of the macroinfauna were used for statistical comparisons (Table 3), the F values fluctuated between 0.03 and 2.29 (1991) and between 0.06 and 5.21 (1992). The *P* values fluctuated between 0.130 and 0.994 during 1991, and between 0.008 and 0.980 during 1992. Thus, as in the case of the sedimentological characteristics, only during the second experimental period (1992) did the *P* values indicate sig-

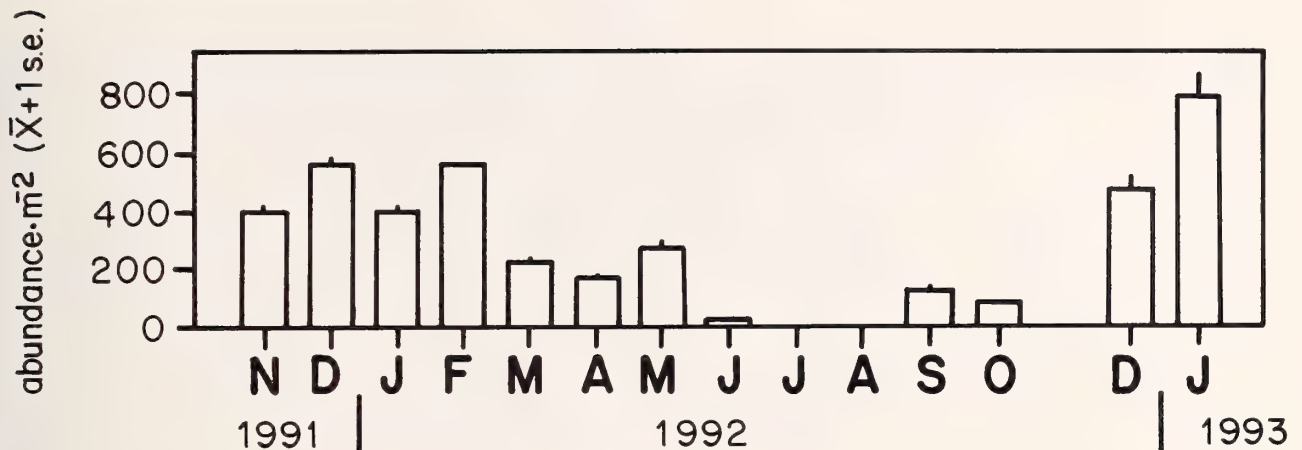


Figure 2

Temporal variability of the population abundance of *C. ovalis* in the sediments of the study area. No samples were collected in November 1992.

nificant difference between the treatments (Figure 6): the abundance of *C. capitata* in control and wall sediments was significantly higher than that calculated in the exclusion sediments ($P = 0.008$, day 60); the abundance of the *Littoridina* species was significantly different when inclusion and exclusion sediments were compared ($P = 0.023$).

The macroinfaunal analyses rendered a total of six species, the most abundant taxa being the ostracod *Cyprideis beaconnensis* Leroy (2–122 ind/4 cm²), the polychaete *Capitella capitata* Fauvel (1–34 ind/4 cm²), and a species of *Littoridina* (0–4 ind/4 cm²) (Figures 5, 6). Other species were occasionally recorded: the polychaetes *Perinereis gualpensis* Jeldes, *Prionospio (Minuspio) patagonica* Augener, and the amphipod *Paracorophium hartmannorum* Andrés. No species composition difference was detected when the treatments were compared.

The total abundance of the macroinfauna (up to 137 ind/4 cm²) decreased toward the end of the summer of 1991, following the trends of *C. beaconnensis* and *C. capitata* abundance (Figures 5, 6). Species richness (two to four species) did not show temporal variability.

Sediment comparisons: In the comparison of sediments with snail trails versus undisturbed sediment, sand, aggregates, mud, water, organic matter, and chlorophyll *a* contents showed some differences in magnitude (Figure 7). However, only the chlorophyll *a* content was significantly lower ($P = 0.001$) in disturbed (87.2 ug/g) versus undisturbed sediment (101.1 ug/g).

DISCUSSION

Most of the results of the field experiments suggest that *C. ovalis* does not affect the structure of the intertidal

Table 1

Mean sizes in mm of the cohorts of *C. ovalis*, detected by "Modal Progress Analysis" (MPA). Mean monthly growth rates are also presented.

Date	Cohort 1990		Cohort 1991		Cohort 1992	
	Size	Growth	Size	Growth	Size	Growth
November 1991	15.764	—	5.224	—	—	—
December	16.665	0.901	5.448	0.224	—	—
January 1992	16.884	0.219	6.902	1.545	—	—
February	17.020	0.136	7.852	0.950	—	—
March	18.355	1.335	10.103	2.251	—	—
April	—	—	11.908	1.805	—	—
May	—	—	12.973	1.065	—	—
September	—	—	16.273	0.825	—	—
October	—	—	16.500	0.227	—	—
December	—	—	16.712	0.106	5.423	—
January 1993	—	—	17.593	0.881	7.545	2.122

Table 2

Summary of variance analysis carried out with the sedimentological characteristics. Degrees of freedom were 3–12 for the period 1991 and 3–20 for the period 1992. The values of F and P (in parentheses) are given in the columns below each sedimentological characteristic. Asterisks indicate significant difference in sand content among sediments of control versus inclusion treatments (days 8 and 90) (cf. Figure 4).

	Sand	Aggregates	Mud	Water	Org. matter	Chlorophyll <i>a</i>
1991–start	0.59 (0.633)	1.19 (0.362)	1.19 (0.362)	0.74 (0.550)	1.30 (0.325)	2.58 (0.102)
day 6	0.43 (0.737)	0.05 (0.984)	0.15 (0.928)	0.69 (0.579)	0.19 (0.900)	0.26 (0.853)
day 11	0.24 (0.863)	0.62 (0.616)	0.18 (0.905)	1.57 (0.249)	0.09 (0.965)	2.59 (0.101)
day 30	1.32 (0.313)	0.39 (0.762)	0.46 (0.714)	1.23 (0.346)	0.53 (0.672)	1.71 (0.217)
1992–start	0.40 (0.755)	0.59 (0.629)	0.82 (0.500)	0.06 (0.979)	0.62 (0.608)	0.36 (0.783)
day 3	0.47 (0.708)	0.20 (0.894)	0.17 (0.919)	1.32 (0.297)	0.19 (0.901)	2.38 (0.100)
day 8	5.58 (0.006)*	1.62 (0.217)	0.68 (0.576)	1.44 (0.260)	0.02 (0.996)	0.49 (0.700)
day 30	0.49 (0.693)	0.21 (0.888)	0.11 (0.953)	0.71 (0.560)	0.61 (0.620)	1.60 (0.222)
day 60	0.28 (0.840)	1.03 (0.400)	1.02 (0.406)	1.18 (0.341)	0.33 (0.802)	0.17 (0.913)
day 90	3.55 (0.037)*	2.95 (0.062)	2.06 (0.144)	0.31 (0.821)	0.79 (0.513)	0.45 (0.720)

sediment and macroinfauna in the Lingue River estuary. The experiments were set up intuitively expecting the dramatic changes that occur with the manipulation of some species (Paine, 1980). However, these changes did not occur or were trivial, leading to rejection of the hypothesis. In addition, the experiments did not detect the existence of confounding effects such as artifacts; i.e., no differences were found between the sediment of the control and wall treatments on any occasion (cf. Hall et al., 1990).

The results of the comparisons of sediment with and without feeding trails indicate that *C. ovalis* indeed affects the phytobenthic biomass on a time scale of minutes or hours. However, these effects do not persist longer than one tidal cycle. These results differ from those described by Pace et al. (1979), who detected effects of *Ilyanassa obsoleta* on the phytobenthos only after the third day and

lasting until at least 10 days after the start of their experiments. Laboratory studies have detected a negative effect on the phytobenthos by a high abundance of *I. obsoleta*, but a positive effect when abundance of the gastropod was lower (Connor et al., 1982). A similar relationship characterized the interaction between *Hydrobia totteni* and the phytobenthic standing-stock in tidal flats of Long Island, New York (Levinton & Bianchi, 1981).

Our experiments were carried out during summer periods characterized by the presence of greater abundance, higher growth rates of gastropods, and more trails on the sediment surface (personal observation). Later in the year because the snails are present in minor abundance, we can expect similar or smaller effects than those detected with these experiments (cf. Hunt et al., 1987; Cammen, 1989; Peterson & Black, 1993).

Possible explanations for the absence of effects of *C.*

Table 3

Summary of variance analysis carried out with faunal characteristics. Degrees of freedom were 3–12 for the period 1991 and 3–20 for the period 1992. The values of F and P (in parentheses) are given in the columns below each faunal characteristic. Asterisks indicate significant difference in faunal abundance. Among *C. capitata* in sediments of the wall and exclusion treatments versus that in control sediments (day 60); and between the abundance of *Littoridina* sp. in sediments of the exclusion versus that in inclusion sediments (day 90) (cf. Figure 6).

	<i>C. beaenensis</i>	<i>C. capitata</i>	<i>Littoridina</i> sp.	Total abundance	Spp. richness
1991–start	0.79 (0.523)	0.35 (0.788)	0.22 (0.879)	0.51 (0.685)	0.49 (0.699)
day 6	0.44 (0.734)	0.23 (0.870)	0.38 (0.773)	0.31 (0.816)	0.19 (0.896)
day 20	0.70 (0.570)	0.03 (0.994)	0.47 (0.706)	0.46 (0.717)	0.36 (0.781)
day 30	0.36 (0.787)	2.29 (0.130)	0.41 (0.746)	0.45 (0.724)	0.48 (0.705)
1992–start	0.39 (0.761)	0.93 (0.444)	1.01 (0.412)	0.46 (0.712)	0.48 (0.703)
day 3	1.78 (0.184)	0.47 (0.704)	1.97 (0.151)	1.01 (0.408)	0.06 (0.980)
day 8	0.37 (0.775)	0.08 (0.972)	3.08 (0.051)	0.22 (0.885)	2.75 (0.070)
day 15	0.76 (0.531)	0.37 (0.777)	0.51 (0.679)	0.55 (0.654)	1.43 (0.264)
day 30	0.79 (0.515)	0.60 (0.622)	0.34 (0.795)	0.76 (0.533)	0.68 (0.578)
day 60	2.14 (0.127)	5.21 (0.008)*	1.11 (0.368)	2.88 (0.061)	1.57 (0.228)
day 90	0.60 (0.621)	1.03 (0.401)	3.97 (0.023)*	0.99 (0.416)	0.79 (0.512)

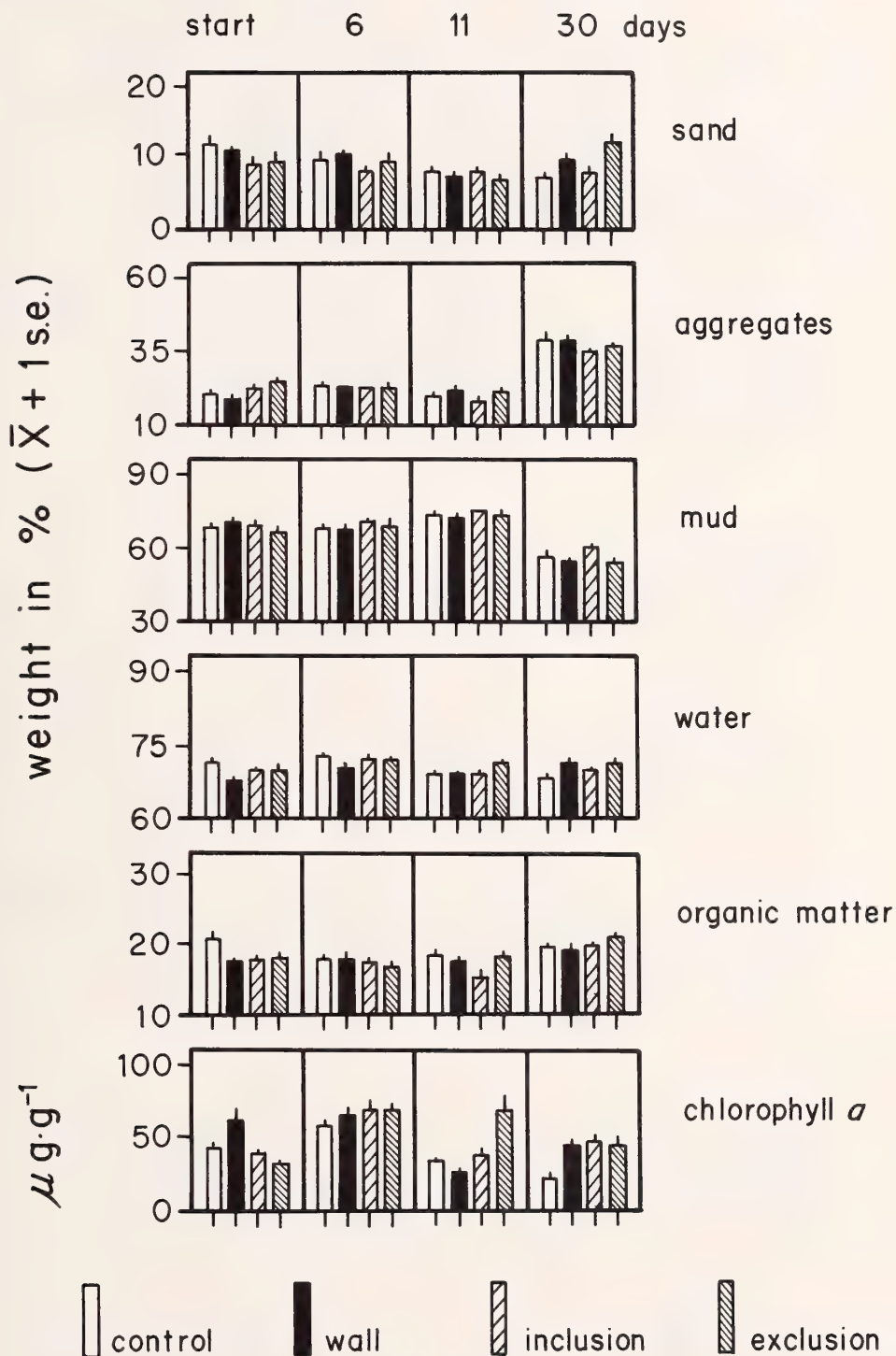


Figure 3

Sedimentological characteristics resulting from field experiments carried out in the summer of 1991. Asterisks indicate the days when significant differences among the treatments ($p < 0.05$) were detected (see Table 2).

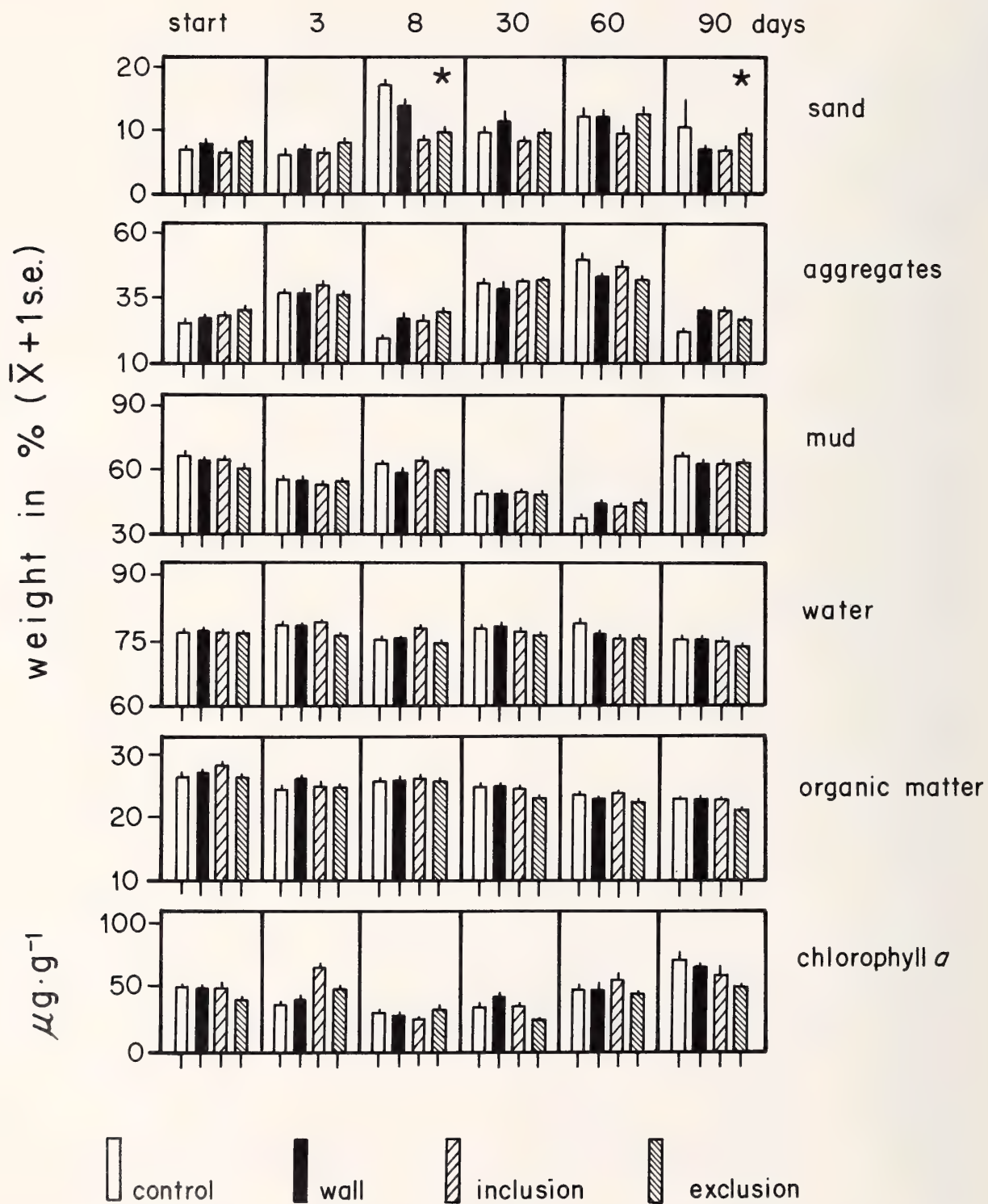


Figure 4

Sedimentological characteristics resulting from field experiments carried out in the summer of 1992. Asterisks indicate the days when significant differences between the treatments ($p < 0.05$) were detected (see Table 2).

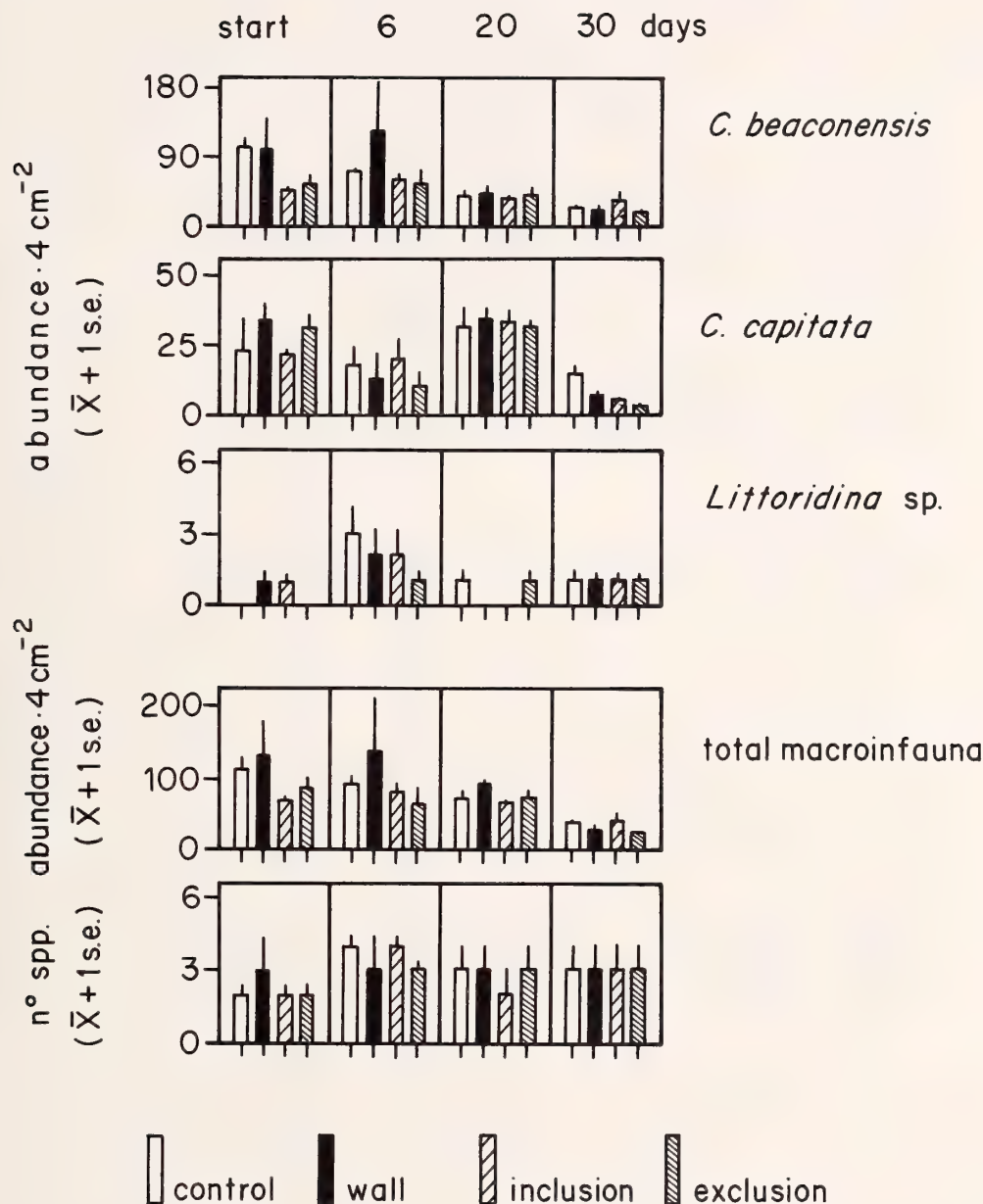


Figure 5

Abundance of *C. beaconensis*, *C. capitata*, the species of *Littoridina* genus, and total macroinfauna and species-richness resulting from field experiment, carried out in the summer of 1991. Asterisks indicate the days when significant differences between the treatments ($p < 0.05$) were detected (see Table 3).

ovalis include factors that regulate the production of trails and others that inhibit their potential effects. The population size of *C. ovalis* and the consequent feeding pressure which it exerts could be below the level at which food becomes a limiting resource (see Peterson & Black, 1987). The high availability of nutrients in the area should allow an increase in population size and age reached by individuals (cf. Forbes & Lopez, 1986). How-

ever, more than two cohorts were never directly observed simultaneously, while individuals reached an age of at least 18 months. By comparison, in the same genus ages of 2 years and two or more reproductive periods have been described for *C. gibbosa* in an Argentine freshwater reserve located at a latitude comparable to the Lingue River estuary (Bosnia et al., 1990).

Other factors can diminish the possible effects of the

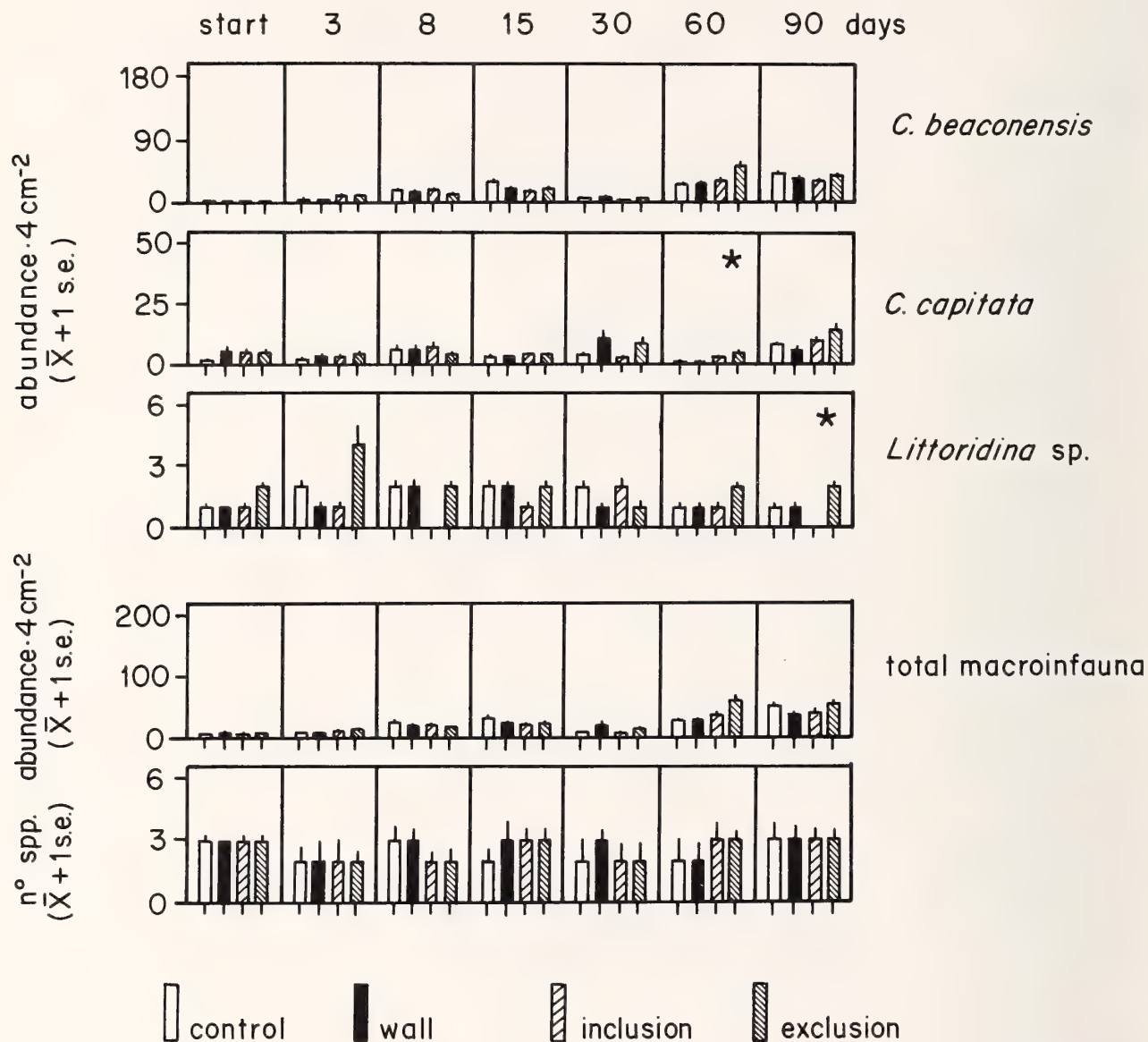


Figure 6

Abundance of *C. beaconensis*, *C. capitata*, the species of *Littoridina* genus, and total macroinfauna and species-richness resulting from field experiment carried out in the summer of 1992. Asterisks indicate the days when significant differences between the treatments ($p < 0.05$) were detected (see Table 2).

Table 4

Summary of variance analysis carried out with the sedimentological characteristics of sediments in areas with and without trails of *C. ovalis*. Degrees of freedom were 1–38. The values of F and P (in parentheses) are given in the columns below each sedimentological characteristic. Asterisk indicates significant difference in the contents of chlorophyll *a*. (cf. Figure 7).

Sand	Aggregates	Mud	Water	Org. matter	Chlorophyll ^a
3.83 (0.058)	1.42 (0.241)	1.80 (0.187)	3.23 (0.080)	0.03 (0.873)	12.40 (0.001)*

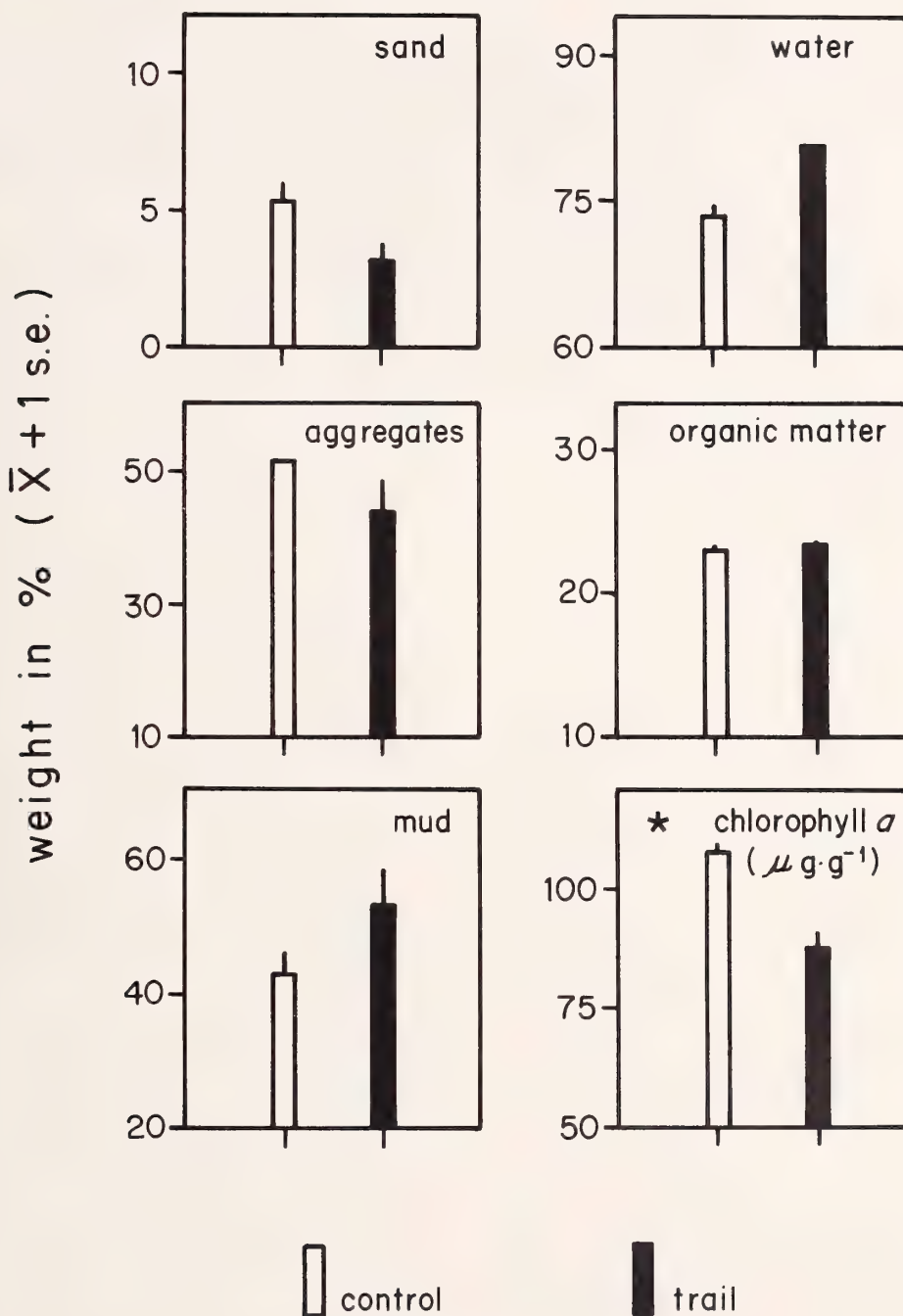


Figure 7

Sedimentological characteristics in areas with and without trails (control sediments) of *C. ovalis*. Asterisk indicates the existence of significant differences ($p < 0.05$).

trails and explain the lack of lasting and cumulative effects of *C. ovalis*. The tides import, resuspend, redistribute, and export sediments (Eisma & Li, 1993), fecal aggregates (Risk & Moffat, 1977; Taghon & Jumars, 1984), phytobenthos (de Jonge & van Beusecom, 1995), and or-

ganisms of the macroinfauna (Butman et al., 1988a,b). The tides are also associated with bottom diatom proliferation and recolonization (Admiraal & Peletier, 1987) on recently altered patches of sediment (trails).

The macroinfauna could also be responding to the local

disturbance exerted by *C. ovalis*. Capitellid species, for example, can rapidly recolonize recently altered sediment patches, supposedly in response to nutrient availability and the temporary absence of competing species (Tsutsumi et al., 1990). In addition, other species can escape mechanical disturbance of sediment by burrowing to deeper layers in the sediment (refuge), avoiding the effects of the disturbance (Roberts et al., 1989).

Surprisingly, *C. ovalis* did not affect the texture or water content of the sediment, which suggests that this species alters neither the resuspension nor the stability of the substrate (cf. Rhoads & Boyer, 1982). This differs from the findings of Boyer (1980) who demonstrated through-out laboratory experiments that a larger snail (*Polinices duplicatus*) was able to destabilize the sediment of a tidal flat in Massachusetts, USA. The effects of *P. duplicatus* were first observed after 24 hours of experimentation and remained until at least 4 days after the snails were excluded. Thus, it seems that *C. ovalis* does not form part of the biological component that affects water-sediment interaction (see Meadows & Tait, 1989; Paterson, 1989; Paterson & Daborn, 1991), at least in the time period studied.

The role of *C. ovalis* contrasts with what is currently known about gastropods such as *I. obsoleta*, which in terms of size and habitat appears to be a functionally comparable species. *I. obsoleta* affects the structure of macroinfaunal (Hunt et al., 1987; Frid & James, 1988), bacterial (Bianchi & Levinton, 1981), and phytobenthic (Pace et al., 1979; Lopez & Levinton, 1987) communities. These differences could result from factors such as dietary flexibility (Feller, 1984), behavioral aspects (Cranford, 1987), and the existence of intrapopulation interactions (Levinton, 1985; Forbes & Lopez, 1986). The absence of previous work on the natural history of *C. ovalis* remains the main obstacle to identifying the role of this species and the degree of its similarity to *I. obsoleta* and other species around the world.

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Designation of Lectotype for *Haliotis crebrisculpta* Sowerby, 1914, with a Discussion of *H. clathrata* Reeve, 1846 (*non* Lichtenstein, 1794)

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Abstract. The three syntypes of *Haliotis crebrisculpta* Sowerby, 1914, belong to two species. The figured specimen of Sowerby (BMNH 1919.12.31.19) is designated as lectotype. This species remains known from a single shell from New Caledonia. It is characterized by the eccentric apex (1/7.2 from the posterior margin of the shell) of the oblong shell and its strong spiral cords bearing numerous scales. The other two specimens in the syntype series of *H. crebrisculpta* are referable to *H. clathrata* Reeve, 1846 (*non* Lichtenstein, 1794). *Haliotis clathrata* Reeve has been poorly identified in the literature. It is redescribed on shell, radular, and epipodial characters. *Haliotis clathrata* is not a subspecies of *H. rubra* Leach, 1814, but the fossil *H. tuvuthaensis* Ladd in Ladd & Hofmeister, 1945, is synonymized under it. The species ranges from Madagascar to American Samoa and from southern Japan to the Sydney area of southeastern Australia.

INTRODUCTION

In the family Haliotidae Rafinesque, 1815, approximately 200 species-level taxa have been described, of which 55 species with 11 subspecies are thought to be valid; an encompassing treatment of all those taxa was provided by Geiger (1998a). Several taxonomic issues have recently been addressed (Stewart, 1984; Herbert, 1990; Geiger, 1996, 1998b), but some uncertainties still await treatment. Here we deal with one source of confusion at the species level. The clarification of the taxonomy in this family is necessary for a forthcoming cladistic analysis of the family by DLG.

The identity of *Haliotis crebrisculpta* Sowerby, 1914, has been controversial in the literature. One specimen of the syntype series is here designated as lectotype of *H. crebrisculpta*. The other two specimens are identified as *Haliotis clathrata* Reeve, 1846. As these three specimens are syntypes, the designation of a lectotype is necessary.

In the following, *H. clathrata* refers to the taxon so-named by Reeve (1846) and not the overlooked, senior homonym of Lichtenstein (1794) discussed below and elsewhere (Geiger, 1998b; Geiger & Stewart, in press), unless specifically indicated. The variable *H. clathrata* has also been labeled *H. crebrisculpta*, causing much confusion. Those specimens with more pronounced spiral sculpture tended to be identified as *H. crebrisculpta*, whereas those with more or less radial ridges along the

growth lines have rather been called *H. clathrata*. Kuroda & Habe (1952) went as far as to synonymize *H. crebrisculpta* with *H. clathrata*. The synonymy of *H. clathrata* with *Haliotis rubra* Leach, 1814, first suggested by Sowerby (1882), is without merit as discussed below.

Due to the long-standing confusion with respect to the identity of *H. clathrata*, we provide here a detailed redescription of the shell, report for the first time the morphology of the epipodium and the radula, and discuss the geographical distribution.

MATERIALS AND METHODS

The radulae of *H. clathrata* from dry specimens, which were rehydrated in 75% ethanol, were isolated in 4 M NaOH; the NaOH solution was changed daily until the body was completely dissolved. For wet-preserved specimens, the radula was dissected out, washed in water, cleaned with 4 M NaOH overnight, washed twice in water, dehydrated through two washes in 100% ethanol, mounted while drying in air on double-sided carbon adhesive (Ted Pella 16084–2) on a coin of 24 mm diameter, which in turn was mounted on a Cambridge stub with colloidal graphite, sputter-coated with gold, and viewed at an accelerating voltage of 10 kV and a probe current of 200 pA on a Cambridge 360 scanning electron microscope using the secondary electron detector.

Epipodial characters from four specimens of *H. clathrata* were assessed. A representative piece was cut from the preserved animal, washed in 100% ethanol, and trans-

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ferred into 100% hexamethyldisilazane (HMDS: Polyscience). After 1 day the HMDS was changed and the next day the sample was air dried at room temperature. The specimen was mounted with colloidal graphite on a coin (see above). It was either sputter-coated, and viewed at an accelerating voltage of 2–5 kV and a probe current of 100–200 pA, or drawn with a camera lucida attached to a dissecting microscope.

Statistical analysis was performed with Statistica[®] for Macintosh 4.1 (StatSoft, 1994).

Specimens from the following collections were examined: AMNH, American Museum of Natural History, New York; ANSP, Academy of Natural Sciences, Philadelphia; BMNH, The Natural History Museum, London; CASIZ, California Academy of Science, Invertebrate Zoology, San Francisco; DLG, D. L. Geiger collection, Los Angeles; DMNH, Delaware Museum of Natural History, Wilmington; KAS, K. A. Stewart collection, Carmel, California; LACM, Los Angeles County Museum of Natural History; MNHN, Muséum Nationale d'Histoire Naturelle, Paris; NM, Natal Museum, Pietermaritzburg, South Africa; NMW, National Museum of Wales, Cardiff, Wales; RP, Roger Pickery collection, Wilrijk, Belgium; SBMNH, Santa Barbara Museum of Natural History, California; UCMP, University of California Museum of Paleontology, Berkeley; USNM, National Museum of Natural History, Smithsonian Institution, Washington, D. C.

SYSTEMATICS

Haliotis crebrisculpta Sowerby, 1914 (Figure 1A)

H. crebrisculpta Sowerby, 1914:—Sowerby, 1914: 478, pl. 14, fig. 2.—Kaicher, 1981: card no. 2878.

Non H. crebrisculpta (Misidentifications of *H. clathrata*):—Talmadge, 1963: 137, pl. 14, fig. 1.—Hinton, 1972: 1, fig. 4.—Hinton, 1978: 2, fig. 12.—Anon., 1975: 5.—Abbott & Dance, 1983: 22.—Dharma, 1988: pl. 1, fig. 5.—Wilson, 1993: 48, pl. 5 fig. 9 A, B.—Pickery & Steppe, 1995: pl. 5, fig. 4.

Identity of the three syntypes: Specimen BMNH 1919.12.31.19 (Figure 1A) agrees with the original illustration. The other two specimens NMW 1955.158.608 (Figure 1B) and USNM 341787 (Figure 1C) are identified as *H. clathrata* (see below for details).

Designation of lectotype: Sowerby (1914) figured only one specimen in his description of *H. crebrisculpta*, in which he did not mention the number of specimens on which his description was based. He sold two specimens specifically as co-types (= syntypes) of this species (S. Greenhouse, personal communication; A. Kabat, personal communication), one of which is now housed in the NMW, the other in the USNM. The specimen in the BMNH is marked "type" in Sowerby's hand (K. Way, personal communication) and corresponds precisely with

the figure of Sowerby (1914), particularly in the spiral sculpture with its numerous fine lamellae, and the placement of the apex. The description of the shell is somewhat ambiguous as to which shell was being described, possibly owing to the fact that the taxon had been based on three non-conspecific syntypes. The most striking discrepancy is found in the number of open perforations. The original description mentioned four open perforations; the specimen in the BMNH has seven, the one in the USNM has five, and the one in the NMW has four. New Caledonia as the type locality applies for all the three syntypes. The figured specimen (BMNH 1919.12.31.19) is here designated as the lectotype for *H. crebrisculpta* Sowerby, 1914.

This species has not been recollected and remains known from a single shell. Particularly, no specimen could be found in the old or new holdings of the MNHN, known for its long-standing collection effort at the type locality—New Caledonia—through the ORSTOM-program. We recognize that the types of some taxa in the Haliotidae are aberrant specimens of other species. However, no similar case can be made for *H. crebrisculpta* due to lack of indications such as a strong growth mark from an injury, irregularities in the nacre, or a lateral shift of the selenizone. The specimen is not a hybrid, as the characters are not in between any two known species, but occupy a peripheral position in the morphospace of the family. The lectotype is sufficiently distinct to warrant recognition at the species level. It is characterized by its very eccentric apex, oblong shell, and the sculpture consisting of scabrous scales on the strong spiral cords (Table 1). Such a combination of characters is not found in any other abalone species.

Redescription of lectotype (Figure 1A): Shell small (30 mm), oblong, somewhat convex. Apex eccentric at 1/7.2 from posterior margin. Spire entirely hidden under narrow columella in ventral view. Tremata large, somewhat oval, moderately raised, seven open. Dorsal surface with numerous spiral cords of variable strength. Spiral cords with fine, tightly spaced lamellae, forming stronger, upward directed scales at irregular intervals. Stronger scales in more or less radial rows. Color uniform yellow ochre, dull. Nacre milky, dull. No muscle scar.

Comparisons: *Haliotis clathrata* Reeve, 1846 (Figures 1A, B, 2, Table 1). The spiral cords in *H. clathrata* are never as broad and elevated, and never bear scabrous scales such as found in *H. crebrisculpta*. The apex is more centrally located in *H. clathrata*: approximately 1/3.8 versus 1/7.2 from the posterior margin; this comparison is based on shells of similar size (30 mm; Figure 4). Consequently, the shell of *H. crebrisculpta* is a somewhat more oblong than that of *H. clathrata*.

Whitehead (1982) tentatively synonymized *H. dissona* (Iredale, 1929) with *H. crebrisculpta*. As we are unclear on what species concept of *H. crebrisculpta* had been

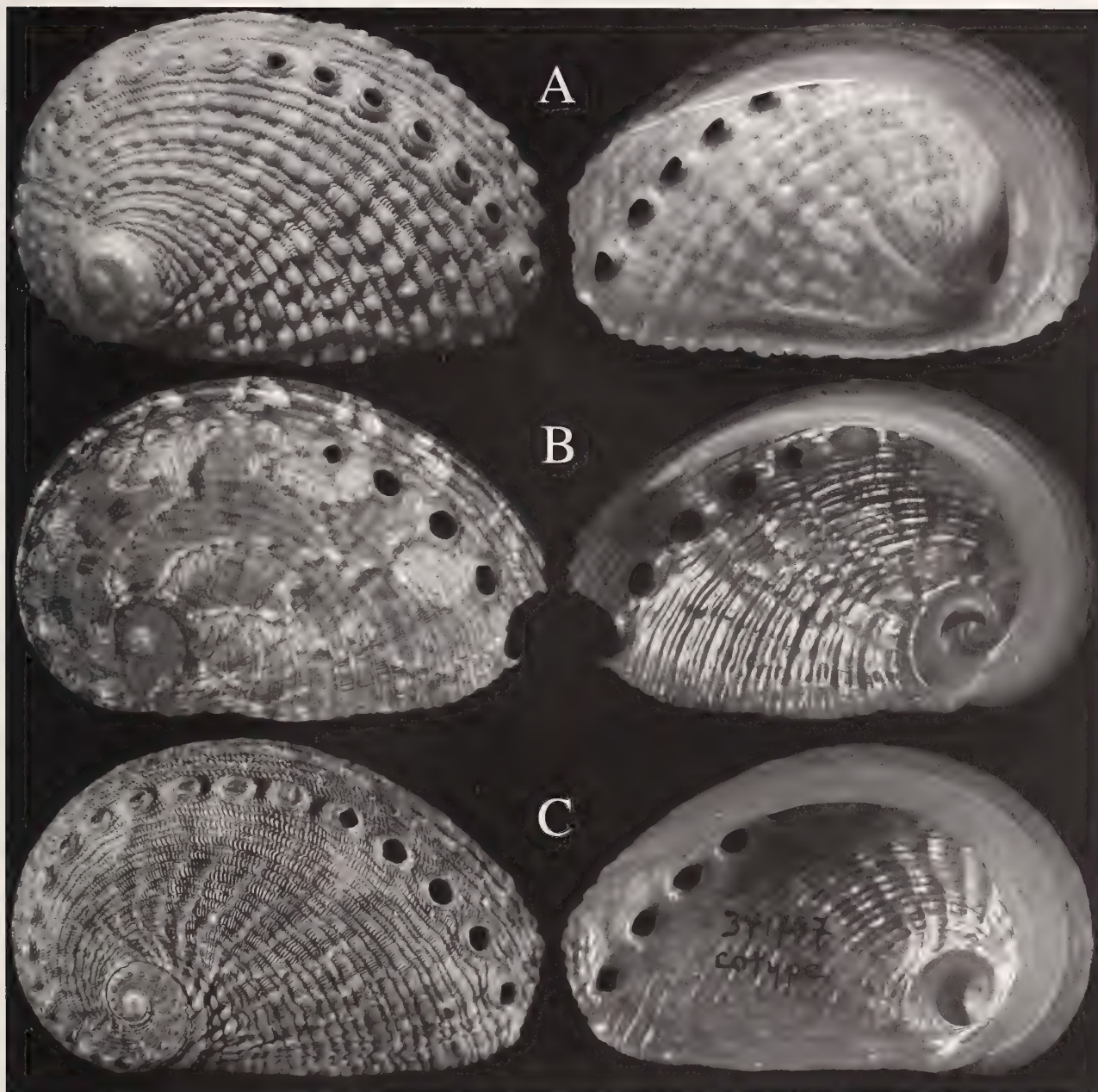


Figure 1

A. Lectotype of *Haliotis crebrisculpta*. New Caledonia. BMNH 1919.12.31.19. Length: 30 mm. B. *H. clathrata*, specimen from syntype series of *H. crebrisculpta*. New Caledonia. NMW 1955.158.608. Length: 30 mm. C. *H. clathrata*, specimen from syntype series of *H. crebrisculpta*. New Caledonia. USNM 341787. Length: 32 mm.

used by Whitehead (1982), we could only speculate on the validity of the statement. We agree with Talmadge (1961) that the status of *H. dissona* is unresolved, because the type specimen is badly worn and fairly small (22 mm).

Haliotis dohrniana Dunker, 1863 (Figure 3A). This species has been described from New Caledonia and is

here tentatively recognized. It has a broad, scattered distribution in the western Pacific, but is a rare, poorly known species. It has a similar overall shape of the shell, but the apex is somewhat less eccentric. The sculpture of *H. dohrniana* does not include scabrous scales, but fine spiral cords with some occasional larger bumps, the latter not being found in *H. crebrisculpta*.

Table 1

Distinguishing shell characters among *Haliotis clathrata*, *H. crebrisculpta*, and *H. rubra*.

Character	<i>Haliotis clathrata</i>	<i>Haliotis crebrisculpta</i>	<i>Haliotis rubra</i>
Post-juvenile shape	oblong	oblong	round
Shell convexity	flat to moderate	strong	flat to moderate
Aperture	\pm straight	\pm straight	rounded
Spiral threads	fine	thick, square cords	absent to fine
Thread thickness	equal	alternating	irregular
Sculpture on threads	fine to very fine lamellae	strong, scabrous scales	very fine lamellae
Apex quotient	1/3 to 1/4.5	1/7.2	1/3.3
Spire in ventral view	mostly visible	hidden by columella	fully exposed
Maximum size	4 cm	3 cm	16 cm
Color elements	irregular mottling	?	prosocline, off-white flammae
Distribution E-W	E-Africa—W Pacific	New Caledonia	S coast of Australia
Distribution N-S	Okinawa—Sydney	New Caledonia	S Queensland—Tasmania

Haliotis squamosa Gray, 1826 (Figure 3B). For a recent account of this species see Stewart (1984). The very eccentric apex and the lamellae on the spiral cords forming elevated scales are common features of *H. crebris-*

sculpta and *H. squamosa*. However, these scabrous scales appear in an almost random fashion in *H. squamosa*, whereas they are arranged in more or less radial rows in *H. crebrisculpta*. The aperture is curved in *H. squamosa*

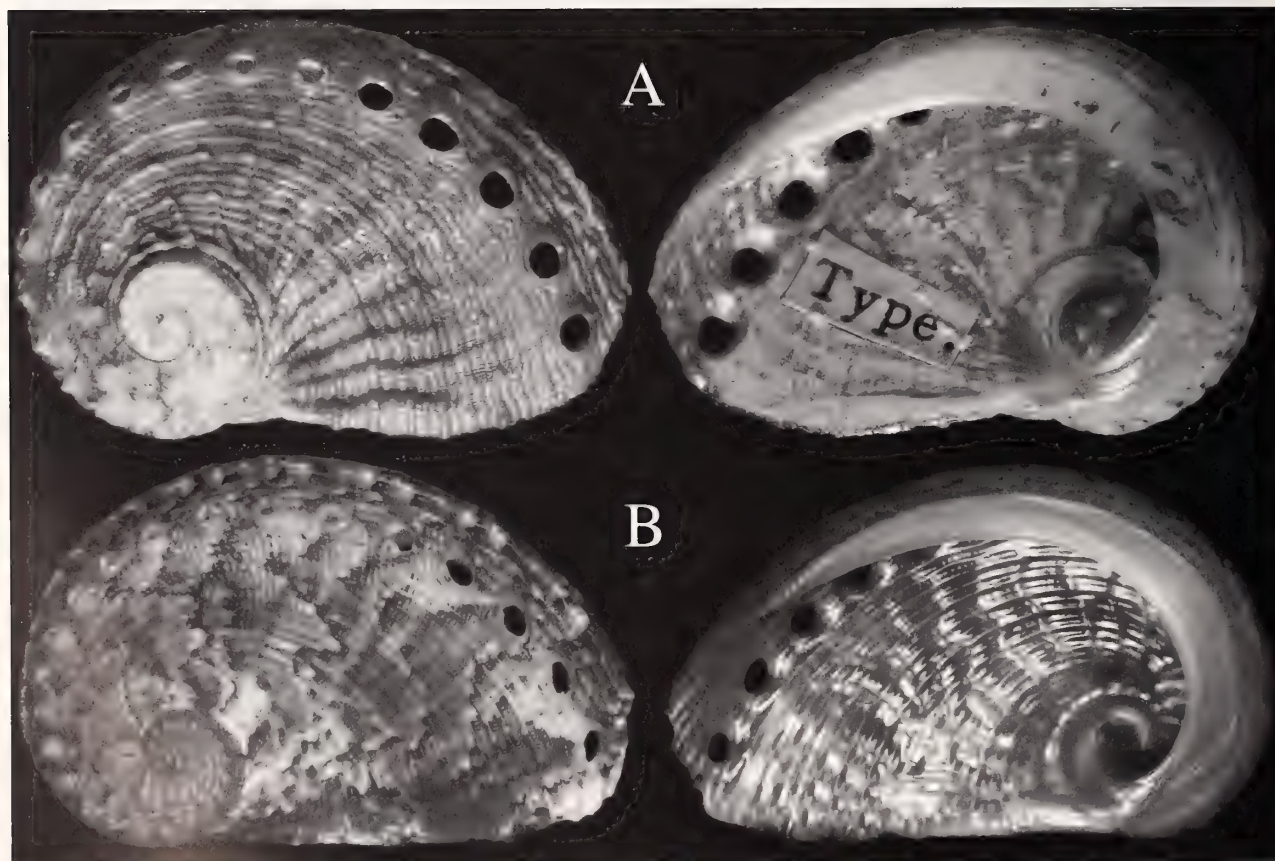


Figure 2

A. Holotype of *Haliotis clathrata*. Baclayon, Island of Bohol, Philippines. BMNH. Length: 23.6 mm. B. *Haliotis clathrata*. Gladstone, Queensland, Australia. Collection R. Pickery, Wilrijk, Belgium. Length: 35 mm.

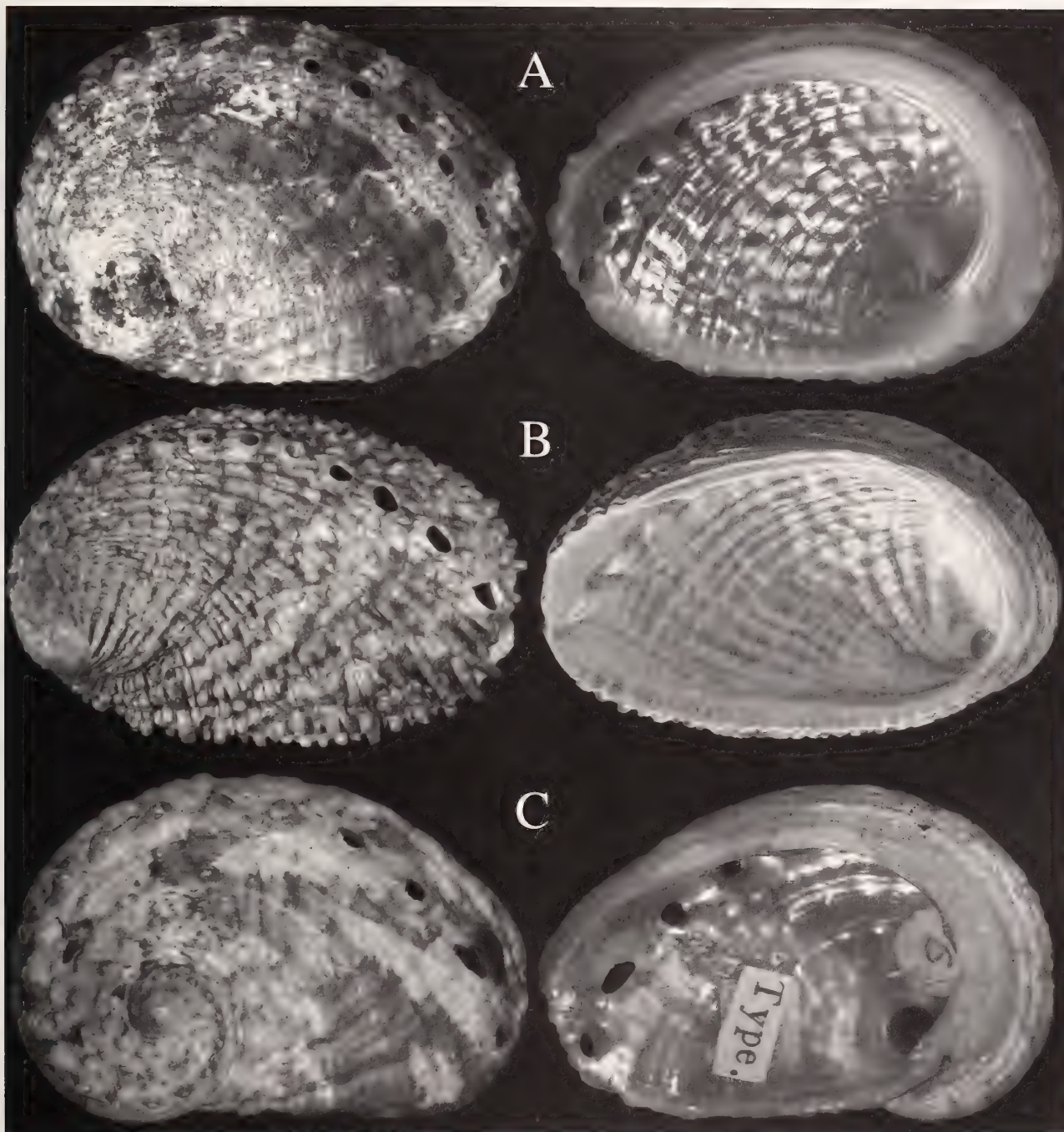


Figure 3

A. *Haliotis dohrniana*. No locality. NMW. Length: 25 mm. B. *Haliotis squamosa*. Dorsal: Holotype. "Australia." NMW. 76 mm. Ventral. Between Fort Dauphin and Monantenina, Madagascar. DLG. Length: 83 mm. C. *Haliotis venusta*. Holotype. "Eastern Seas." BMNH. Length: 38 mm.

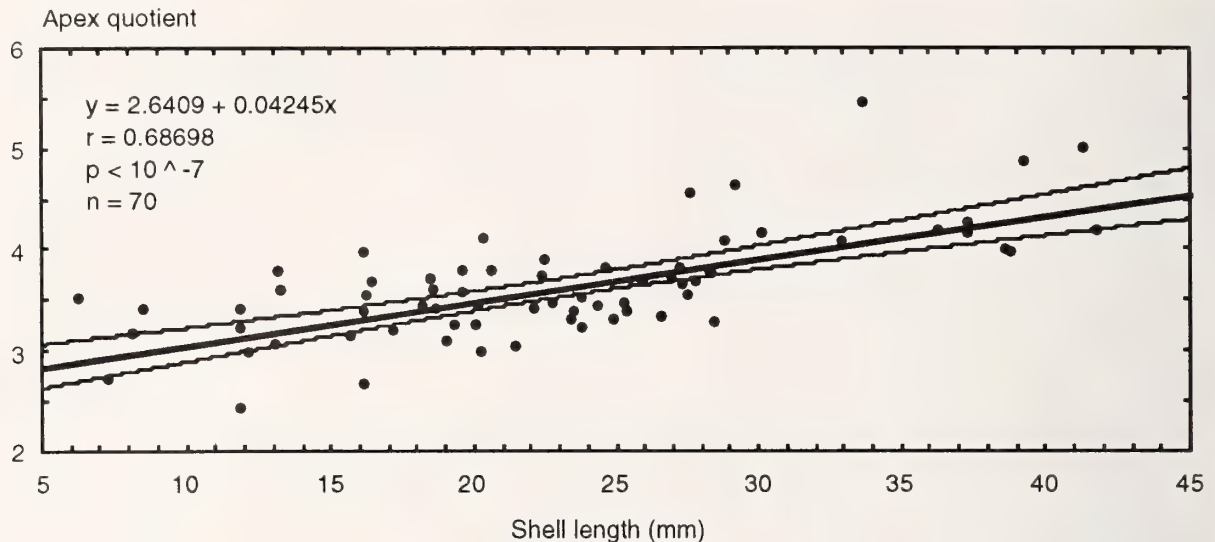


Figure 4

Regression with 95% confidence lines of shell length and apex quotient (shell length/distance of apex from posterior margin of the shell) for *Haliotis clathrata*. The statistical significance of the regression analysis indicates allometric change in the position of the apex to a more eccentric position.

but straight in *H. crebrisculpta*. Moreover, *H. squamosa* has been found only in a restricted part of southern Madagascar with upwelling conditions, whereas *H. crebrisculpta* has a restricted occurrence in tropical New Caledonia.

Geographic distribution: The distribution of *H. crebrisculpta* is limited to the type locality of New Caledonia.

Haliotis clathrata Reeve, 1846 (*non* Lichtenstein, 1794)

(Figures 1B, C, 2, 4–7)

H. clathrata Reeve, 1846:—Reeve, 1846: species 71, fig. 72.—Weinkauff, 1883: 35–36, pl. 29, fig. 7.—Pilsbry, 1890: 117, pl. 5, fig. 26.—Delhaes, 1909: 28–29, fig. 18.—Ladd, 1966 (fossil): 26, pl. 2, figs. 3–5.—Gosliner et al., 1996: 125, fig. 428.

H. tuvuthaensis Ladd in Ladd & Hofmeister, 1945 (fossil): —Ladd & Hofmeister, 1945: 351, pl. 50, figs. E, F

As *H. coccoradiata* Reeve, 1846:—Salvat et al., 1988: pl. 1, fig. 4.

As *H. crebrisculpta* Sowerby, 1914:—Talmadge, 1963: 137, pl. 14, fig. 1.—Hinton, 1972: 1, fig. 4.—Hinton, 1978: 2, fig. 12.—Anon., 1975: 5.—Abbott & Dance, 1983: p. 22.—Dharma, 1988: pl. 1, fig. 5.—Wilson, 1993: 48, pl. 5 figs. 9 A & B.—Pickery & Steppe, 1995: pl. 5, fig. 4.

As *H. crebrisculpta* auct. *non* Sowerby:—Kaicher, 1981: card no. 2832, holotype; card no. 2879.

As *H. gemma* Reeve, 1846:—Pickery & Steppe, 1995: pl. 5, fig. 2.

As *H. rubra* Leach, 1814:—Boone, 1938: 297–298, pl. 113.

As *H. rubra clathrata* Leach, 1814:—Talmadge, 1957: 59–60.

History: *Haliotis clathrata* is well represented in collections. The holotype (Figure 2A) and two paratypes are in the BMNH. *Haliotis clathrata* Lichtenstein, 1794, is an overlooked, senior homonym (Geiger, 1998a, b); we have petitioned the International Commission on Zoological Nomenclature to suppress this name in order to preserve the names of two valid species (Geiger & Stewart, in press). Most records mentioning *H. crebrisculpta* actually referred to *H. clathrata* (e.g., Higa, 1983; Stewart, 1986) because all purported illustrations of *H. crebrisculpta* not involving the here selected lectotype, actually show *H. clathrata*. The figured specimen labeled *H. crebrisculpta* in Talmadge (1961) cannot be identified with certainty, but most likely also represents *H. clathrata*. Kaicher (1981) apparently noted the two different species united under *H. crebrisculpta* and used two cards (nos. 2878, 2879) for this taxon, one as “*Haliotis crebrisculpta* Sowerby” figuring the here selected lectotype BMNH 1919.12.31.19, and one as “*H. crebrisculpta* auct. *non* Sowerby” figuring a specimen conspecific to the syntype specimens in the USNM and the NMW, i.e., *H. clathrata*. The synonym *Haliotis tuvuthaensis* Ladd in Ladd & Hofmeister, 1945, is discussed below under fossil record.

Shell (Figures 1B, C, 2A, B): Shell auriform oblong, flat to moderately convex. Maximum size 4 cm. Apex approximately 1/2.4 to 1/5.4 from posterior margin. Apex more eccentric with increasing shell length (Figure 4). Spiral cords three to four, often more prominent, regularly spaced between suture and tremata. Growth lines fine; every four to five one stronger one, often raised as radial lamella. Lamella from suture but never reaching to tre-

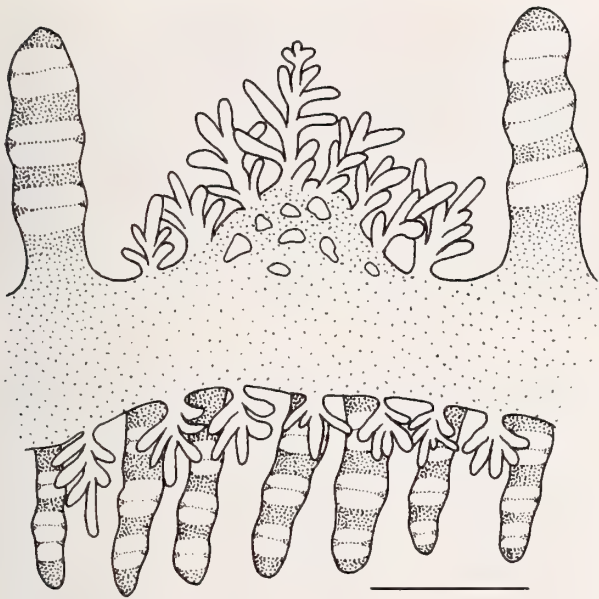


Figure 5

Epipodium of *Haliotis clathrata*. Based on specimen from Comoros, DLG. Scale bar = 1 mm.

mata. Tremata large, slightly oval, somewhat raised, usually four to five open. Spire usually visible in ventral view, sometimes partially obscured by columella of moderate width. Base flat. Nacre brilliant, showing grooves of spiral sculpture. No muscle scar.

Coloration variable. Red tones from bright orange, dull brick red, Bordeaux red to light brown; some also green (particularly specimens from Stanage Bay, Queensland). Uniformly colored specimens rare. Typically with markings in green and off-white, sharp margins and angles, often serrated, often with additional fine, spiral, stippled lines in contrasting color. Markings in prosocline oblique radial pattern, normally not as flammæ. Banding pattern in contrasting coloration always between row of tremata and columella. Width of bands between half and full length between two tremata. For additional color illustrations please refer to '<http://nhm.org/~dgeiger/clathrata.html>'.

Animal: Epipodium (Figure 5) simple for genus. Only dorsal fingered structures and ventral tentacles. Undulating epipodial fold absent, face bare of any structures.

Radula (Figure 6) (for terminology see Geiger, 1996). Cutting edge of rachidian and lateral tooth 1 slightly bent to posterior. Primary ridge of lateral tooth 1 convex, continuous with cutting edge. Secondary ridge attached to main part at approximately $\frac{1}{5}$ to cutting edge forming angle of approximately 45° with primary ridge. Lateral teeth 3 and 4 with single denticle on outer margin of cusp. Lateral tooth 5 with one to four denticles. Cusps of marginal teeth symmetrically denticulated.

Habitat: The species has been found from 0 to 75 m depth, most frequently between 2 and 15 m. It is normally associated with coral reefs and lagoons.

Comparisons: The distinction between *H. clathrata* and *H. crebrisculpta* is discussed above under the latter species and is summarized in Table 1.

Haliotis clathrata is very similar to *Haliotis venusta* Adams & Reeve, 1848 (Figure 3C), in respect to the overall shape of the shell, the numerous spiral cords, the large and somewhat elevated tremata, and the type locality being "Eastern seas" (Adams & Reeve, 1848: 69). However, no trace of the radial lamellæ can be found. Material resembling the type specimens of *H. venusta* is very rare, and we have not found any intermediate specimens of *H. clathrata* and *H. venusta*. We adopt here a conservative position and prefer to keep these two taxa separate until more material of *H. venusta* becomes available. *Haliotis venusta* has been illustrated in the following publications: Adams & Reeve, 1848: 69, pl. 23, figs. 5 a, b; Weinkauff, 1883: pl. 29, fig. 3; Sowerby, 1882: fig. 55; Kaicher, 1981: card 2843.

Haliotis clathrata Reeve, 1846, is not a juvenile *H. rubra* Leach, 1814; for illustrations of *H. rubra* see Hinton (1978) and Abbott & Dance (1983) [both as *H. ruber*]; Hinton (1978), Wells & Bryce (1985), Wilson (1993) [all as *H. conicopora*]. The spelling *H. ruber* in some works is incorrect for *H. rubra*: the adjectival species epithet must be inflected to the feminine of the genus *Haliotis*. Sowerby (1882:31), Pilsbry (1890:117), Cotton & Godfrey (1933), and Cotton (1959) referred to *H. clathrata* as a young *H. naevosa* Martyn, 1784, which is an unavailable synonym (ICZN, 1957: Opinion 456) of *H. rubra*. Boone (1938) and Wagner & Abbott (1978) repeated the synonymy between *H. clathrata* and *H. rubra*, and Talmadge (1957, 1963) called the former a variety of the latter. Weinkauff (1883:35) first listed *H. clathrata* as a juvenile *H. rubra* (as *H. naevosa*), but revised his opinion on pages 80 and 83 ("Nachträge und Berichtigungen": postscripts and rectifications), and stated that the two taxa are not synonymous, but valid species. Delhaes (1909:29) explicitly contradicted the opinion of Pilsbry (1890) that *H. clathrata* represented a juvenile *H. rubra*, and separated *H. clathrata* from *H. rubra* (as *H. naevosa*) giving a differential diagnosis for the two species. Wilson (1993) also questioned the synonymy between the two species, and agreed with Whitehead (1982) that *H. clathrata* needed further study.

Haliotis rubra is a temperate species distributed from Jervis in New South Wales to Freemantle in southern Western Australia, and in Tasmania (Figure 7) (Wells & Bryce, 1985; Ludbrook & Gowlett-Holmes, 1989; Prince & Shepherd, 1992; Wilson, 1993); it includes records of *H. conicopora* Péron, 1816, which has been shown to be only a variation/ecomorph of *H. rubra* (Brown, 1993; Lee & Vacquier, 1995). *Haliotis clathrata*, however, is found

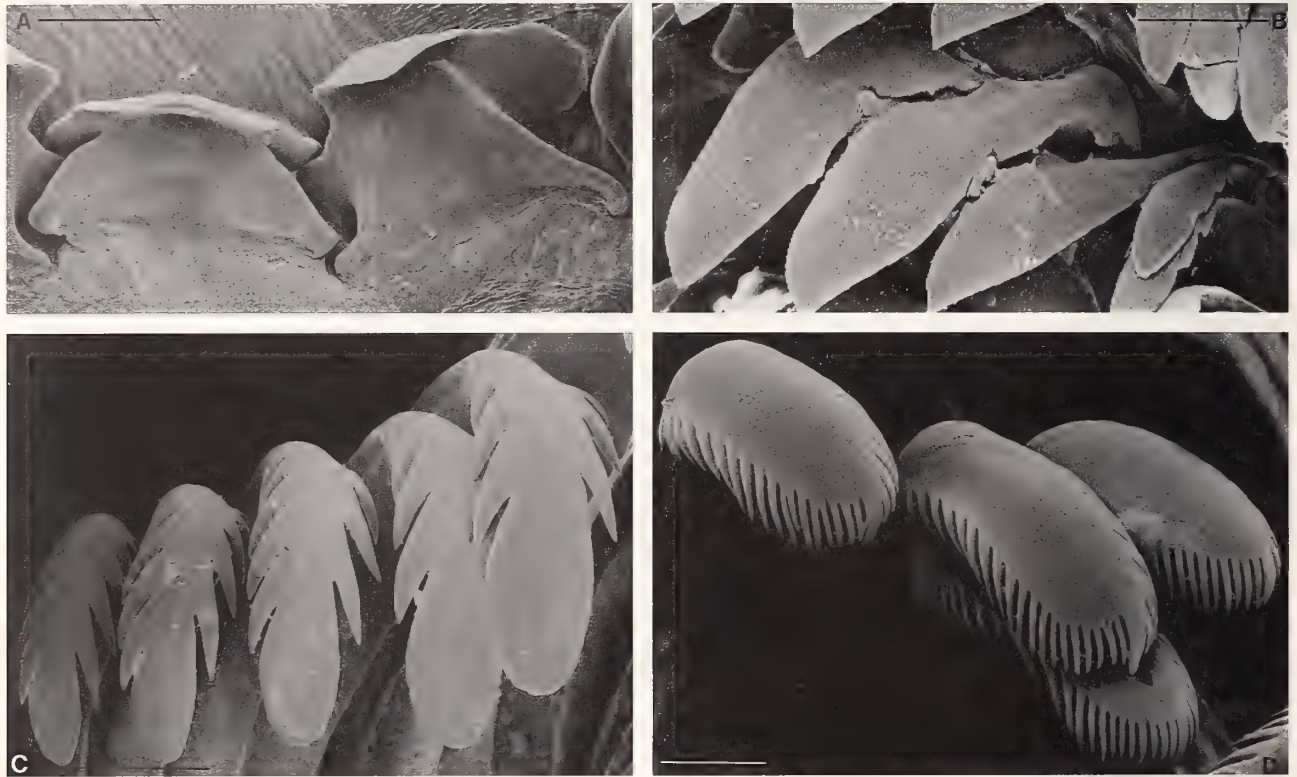


Figure 6

Radula of *Haliotis clathrata*. Based on specimen from Comoros, DLG. A. Rachidian tooth and lateral tooth 1. Scale bar = 50 μm . B. Lateral teeth 3 to 5 and innermost marginal teeth. Scale bar = 50 μm . C. Intermediate marginal teeth. Scale bar = 25 μm . D. Outer marginal teeth. Scale bar = 5 μm .

mostly in the tropical Pacific (Figure 7). *Haliotis rubra* is a large species reaching approximately 16 cm in diameter, and is commercially harvested (Prince & Shepherd, 1992); a young specimen (41.3 mm) was described as *Haliotis ancile* Reeve, 1846. The shell of *H. clathrata* is much smaller, growing only to approximately 4 cm. The surface of the shell in *H. rubra* may either be entirely flat, or it may be undulated, but it never has any lamellae as in *H. clathrata*. The growth lines are always fine and evenly spaced in *H. rubra*, but *H. clathrata* shows the pattern described above. *Haliotis rubra* retains its round form at all growth stages, whereas *H. clathrata* usually is more or less round as a juvenile (< 15 mm) but gets more elongated as it grows larger (Figure 4). This directional change of shape is an invariant character of abalone with oblong shells. A latitudinal gradient in shell shape is equally unlikely. Species with an extensive range (e.g., *H. varia* Linnaeus 1758) do not have such a changes in shape. Additionally, no species in the Haliotidae has a distribution spanning from tropical to temperate faunal regions. Thus, there is no evidence that *H. clathrata* is a juvenile of *H. rubra*. The distinguishing characters between *H. clathrata* and *H. rubra* are summarized in Table 1.

Fossil records: Fossil specimens of *H. clathrata* have been found in the Indo-Pacific, by Ladd (1966) in the Pliocene and Pleistocene of Guam and in the Miocene of Tinian in the Mariana Group, and by Ladd & Hofmeister (1945) in the lower Miocene of Fiji. The latter report described the single specimen at hand as *H. tuvuthaensis*. It is distinguished by the author through the absence of radial folds in the internal mold; otherwise *H. tuvuthaensis* agrees with *H. clathrata* (this study). As the stronger growth lines in *H. clathrata* do not always form radial lamellae (see Figures 1B, C), *H. tuvuthaensis* is a form of *H. clathrata*, and is here synonymized with it. Ladd (1966) compared *H. tuvuthaensis* to *Haliotis ovina* Gmelin, 1791. *H. ovina* is much rounder in its general shape, has a broader columella and more elevated tremata, hence, can be clearly separated from *H. clathrata*.

Talmadge (1963) pointed out the similarity between the fossil *Haliotis powelli* described by Fleming (1952) from the Pleistocene of New Zealand and *H. clathrata* (as *H. crebrisculpta*). We do not agree with Talmadge's (1963) opinion as *H. powelli* is a rather flat species and the general shape of the shell is more rounded; particularly the apertural rim is distinctly curved outward (Lee et al.,

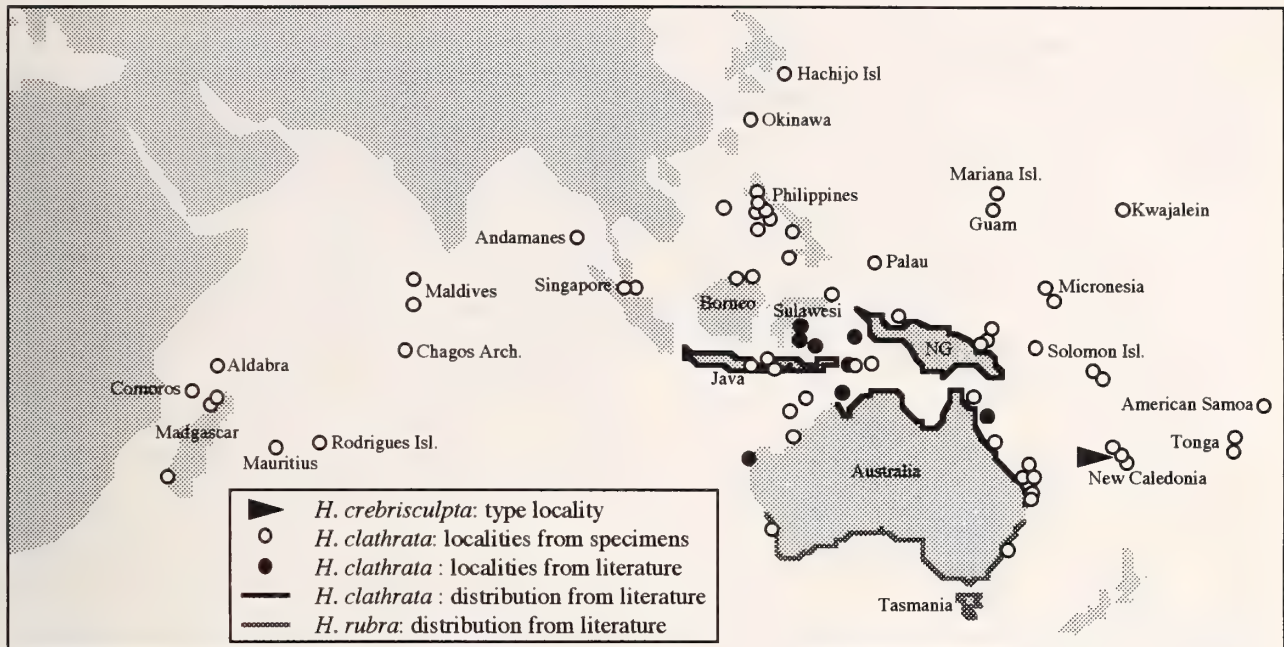


Figure 7

Distribution of *Haliotis crebrisculpta*, *H. clathrata*, and *H. rubra*, based on records herein, and the literature. NG: New Guinea. Localities: based on individual specimen data, either from collections or from illustrations with specific data. Distribution: range indication not based on listed specimens.

1983; Beu & Maxwell, 1990), whereas in *H. clathrata* it is more or less straight. From this limited evidence, the localities for fossil *H. clathrata* are in agreement with its present day distribution.

Geographic distribution: The species is known from literature records in the shallow water of the central and eastern Pacific region from the Hachijo Jima group off southern Japan, Singapore, Indonesia (Bali, Sulawesi, Ambon), Papua New Guinea, Queensland to Western Australia (Scott Reef), and New Caledonia (Boone, 1938; Talmadge, 1963; Hinton, 1972, 1978; Anon., 1975; Dharma, 1988; Salvat et al., 1988; Wilson, 1993; Baer, 1994; Anon., 1995). Specimens from collections add the following localities within the central and eastern Pacific: Andaman Islands, Philippines, Java, Borneo, Marshall Islands, Federate States of Micronesia, Tonga and Western American Samoa. New records representing a substantial range extension stem from the Indian Ocean, i.e., from the Maldives, Chagos Archipelago, Rodrigues Islands, Aldabra, Comoros, Madagascar, and Kenya. Note that the apparent distributional break for abalone at Cape Comorin, India (cf. Geiger, 1996) is crossed by *H. clathrata*. Only one lot has been found from the mainland coast of Africa, none from the Red Sea or the Persian Gulf. Figure 7 shows the distribution of the species.

Specimens examined: Specimens are listed below in

East-West order. The number after the collection and catalog number refers to the number of specimens in the respective lot; preserved animals are marked with "complete."

KENYA: (BMNH 241, 1). MADAGASCAR: 25 km N of Tulear, Mora Mora Village (KAS, 2). Nosi Bé, N Nosi Komba, Pointe Ambarionaombi (ANSP 258629, 1). SW Nosi Bé, between Ambatoloaka and Madirokely (ANSP 259131, 2). COMOROS: (DLG, 1: complete). Sandy Island, Mayotte (NM J9665, 1). Anjouan (BMNH no #, 1). ALDABRA ATOLL: Picard Isl. (USNM 836531, 1). SEYCHELLES: (BMNH no #, 1). MAURITIUS: Belle Mare (CASIZ 044963, 2: complete). RODRIGUES ISL.: (BMNH, 1). Pt. Mathwesi (DLG, 1; KAS, 1). CHAGOS ARCHIPELAGO: Ile du Coin, Peros Banhos (BMNH, 1). MALDIVE ISL.: Gan Addu Atoll, south reef (BMNH, 1). Helengeli (A. Faucci collection, 23). Ari Atoll, NE of Feridu Island, Islet 5.5 km NE of Feridu Island (ANSP 303927, 1: complete).

ANDAMAN ISL.: 80 km E of S Andaman Island, N end of invisible bank (ANSP 292648, 2). N end Invisible Bank, 45 miles E of S Andaman Island, 11° 23' N, 093° 31' E (ANSP 292648, 2).

SINGAPORE: (BMNH; ANSP 196380, 1: complete). Raffles Light (ANSP 245726, 3). Sentosa (KAS, 1). SOUTH CHINA SEA: Macclesfield Bank (BMNH, 2). MALAYSIA: Borneo, Sabah, Sipidan (KAS, 1). Borneo,

Sabah, Sipidan, Sapi Island (KAS, 1: complete). INDONESIA: NW Nusa Perida, Toya Pakeh (DLG, 1; KAS, 1). Java, Thousand Island, Palau Pelangi (KAS, 1). Java, Pulau-Pulau Seribu Island, off Jakarta Raya, Pelangi and Putri Islets (LACM 86-163, 8). Sulawesi, off Manado, S side Banuken and Siladen Islet (LACM 88-56, 3: 1 complete). Bali (RP, 2). Bali, Lovina Beach, north coast (KAS, 6). Dual Tual (RP, 1). Lesser Sunda Isl., Komodo Isl., Station JEM 87-4 (CASIZ 081123, 1). Ambon, Nus Laut Island (DLG, 1: specimen from Baer, 1994). NEW GUINEA: N coast near Madang, Pig Island (= Tab Island) (CASIZ 086544, 1). 2.5 km SW of Biak Dock-Reef (ANSP 206392, 2: complete). New Britain (RP, 1). New Britain, Rabaul (RP, 3).

PHILIPPINES: Bohol (NMW, 1). Luzon Island, Batangas (CASIZ 081039, 1). Luzon Island, Batangas, Devil's Point (CASIZ, 1). Luzon Island, Batangas, Calatagan (DMNH 205368, 1). Luzon Island, Bataan Province (LACM 74724, 1). Palawan, San Pedro Cove, Linapacan Island (LACM 88-285.21, 1). Palawan, Calamian Group, Batunan Island (LACM 74701, 1). Mindanao Island, Zamboanga, Yellow Beach (KAS, 1). Mindoro Island, Aro Point (KAS, 1). Lubang Island (KAS). Maricaoibo Island, Devil Point (KAS, 1: complete). JAPAN: Okinawa, 1 km WNW of Onna Village (LACM 78-27, 1; LACM 78-29, 1; LACM 79-75, 1). Okinawa, 5 km ESE of Zampamisaki (Bolo Point) (LACM 78-25, 1; LACM 78-100, 1). Okinawa, Serigaki Beach (DLG, 6; AMNH 276888, 3). Okinawa, 1 km S of Kuwae Hospital (USNM 838483, 1). Honshu, Hachijo Island (ANSP 240168, 1).

WESTERN AUSTRALIA: Roebuck Bay (AMNH 220132, 1). NE corner of Seringapatam Reef (DLG, 1). Ashmore Reef (DLG, 1; KAS, 1). Cochburn Sound, Woodman Point (ANSP 358590, 1). QUEENSLAND: Lizard Island (LACM 79-53, 1; LACM 79-55, 1). Stange Bay (KAS, 4; RP, 1; DLG, 1; SBMNH, 1). Great Barrier Reef, Grub Reef (LACM 83-44, 1). Capricorn Island (CASIZ 102571, 3). Swain's Reef (CASIZ 102570, 2). Middle Keppel Island (CASIZ 102572, 3). Great Keppel Island (KAS, 1). South Keppel Island, off Yepoon (CASIZ 102936). Keppel Group, Conical Island (CASIZ 102937). Keppel Bay, Middle Island (KAS, 3). Keppel Bay, Keppel Island (SBMNH, 1). Keppel Bay (SBMNH, 1). Keppel Bay, Pumpkin Island (KAS, 1). Gladstone (RP, 1). Humpy Island (KAS, 3). Moreton Bay (KAS, 1). Carter Reef (DMNH 51383, 1). NEW SOUTH WALES: Botany Bay (SBMNH, 2).

MARIANA ISL.: W Saipan (DLG, 3; KAS, 1). Guam (KAS, 3; AMNH 220127, 2). Guam, Orote Cliffs (AMNH 220528, 1). SOLOMON ISL.: NE side Vanganu Island, Marovo Lagoon, Kokuana Passage, Matui Island (LACM 89-77, 1). Bunana Island (BMNH, 1). Honiara (CASIZ, 1). PALAU ISL. = BELAU: Koror, Malakal Harbor (ANSP 203083, 1). FEDERATE STATES OF MICRONESIA: off Arakabesan Island (ANSP 204544, 1). Upper Mortlocks, Losap Island (DMNH 205366, 1). Ka-

pingamarangi Atoll (UCMP loc. # 13107, 1). Helen Reef, Helen Channel, Round Rock (ANSP 399940, 1).

NEW CALEDONIA: (CASIZ 102935, 1). Central N side, Bogota Reefs (USNM 693386, 1). Grand Reef of Koumac (MNHN sta. 1316, 3; MNHN sta. 551, 1). Passe de Koumac (MNHN sta. 1310, 1). Sector of Belep (MNHN sta. 1217, 1; MNHN sta. 1128, 1). Touaourou (USNM 795269, 1). Cook's Reef (CASIZ 102574). Ile des Pins (KAS, 2). Ile des Pins, Kuto Beach (CASIZ 102494). Noumea, Ilot Charron, Baulari Bay (ANSP 275419, 1). Noumea, Baie de Citron (ANSP 237557, 1). Noumea, Baie Ouemo (DMNH 19675, 1; ANSP 271204, 1). Noumea, Touho, Koe Reef (DMNH 69885, 1). Noumea, Touho (ANSP 238033, 1). Sector of Touho (MNHN sta. 1264, 1; MNHN sta. 1271, 1). Bourail (AMNH 107198, 1). Ouen Island, Prony Bay (MNHN sta. 232, 1). Sector of Yaté (MNHN sta. 735, 1). N. O. "Alis" Campagne SMIB 5, 23° 25' S, 168° 05' E (MNHN sta. DW99, 1).

MARSHALL ISL.: Upper Mortlocks, Losap Island (DMNH 205366, 1). Kapingamarangi Atoll (UCMP loc. # 13107, 1). Kwajalein (KAS, 1). Kwajalein, West Reef (DLG, 2; KAS, 4). Kwajalein, Carlson Island (KAS, 3; KAS, 1). Eniwetok Atoll (AMNH 92485, 1). TONGA: Ha'apai Group, Cornfield and Campbell (CASIZ 102573, 1: complete). Vava'u Group, SW Vava'u Island S end Pangaimota Island cliff at W end of Maugai (LACM 86-220, 1). Vava'u Group, N side Nuapupa Island Outside of lagoon (LACM 85-89, 1). Vava'u Group, between Longitau Island and Vaka'eitu Island (LACM 85-90, 1). Eua Island Aa'a Luma Beach (KAS, 1). WESTERN SAMOA: Savaii Island Mataatu Harbor, Eastern Reef (AMNH 178945, 1). AMERICAN SAMOA: Fagan Bay (KAS, 2).

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NOTES, INFORMATION & NEWS

***Lioconcha (Sulcilioconcha) caledonensis* sp. nov., a Species of Veneridae (Bivalvia) from New Caledonia**

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Introduction

Careful re-examination of existing collections is sometimes the source of new taxa (Lamprell & Stanisc, 1996). Eight lots of specimens labelled *Lioconcha (Sulcilioconcha) melhartae* Lamprell & Stanisc, 1996, a venerid species recently described from New Caledonia and taken by extensive sampling programs conducted by the OR-STOM Institute in New Caledonia (Richer de Forges, 1990, 1991), were obtained from the Muséum National d'Histoire Naturelle, Paris. Some specimens differed from *L. (S.) melhartae* and are regarded as a new species, described here.

Materials and Methods

Examination and measurements were done using vernier dial calipers and a 10× magnifying piece. Photographs were prepared by K. Lamprell using a Nikon FM2 camera, SB-21 Nikon Speedlight, AF Micro-Nikkor 105 mm × f/2.8 lens and copy stand.

Abbreviations used in text: lv, left valve; rv, right valve; pv, paired valves, sta., sampling station of OR-STOM Institute in New Caledonia (Richer de Forges, 1990, 1991); MNHN, Muséum National d'Histoire Naturelle, Paris. Shell length is the greatest distance from anterior to posterior margins. Shell height is the greatest distance from the umbo to the ventral margin. Shell width is the greatest distance between the external surfaces of the conjoined left and right valves.

Systematics

The systematic arrangement at generic and subgeneric levels follows that of Keen (1969).

Genus *Lioconcha* Mörch, 1853

Type species: *Venus castrensis* Linnaeus, 1758; subsequent designation by Stoliczka (1870).

Subgenus *Sulcilioconcha* Habe, 1951

Type species: *Cytherea philippinarum* Hanley, 1844; original designation.

Lioconcha (Sulcilioconcha) caledonensis
Harte & Lamprell, sp. nov.

(Figures 1a-c, g-i.)

Description: Shell trigonally ovate, equivalve, inequilateral, moderately inflated, lightweight but sturdy, umbones prosogyrous, slightly inflated, lunule well developed, pear-shaped, raised centrally, striate, defined by a faint impressed line; antero-dorsal margin short, slightly convex dorsally, sharply sloping, widely rounded terminally; postero-dorsal margin slightly convex, sharply sloping, widely convex posteriorly; ventral margin widely convex, incised. Shell to 21 mm in length. Teleoconch smooth, changing to sculpture on the disc 4.2 mm down from the tip of the umbo of a specimen 17.1 mm in height. Shell with fine, distinct, flattened cords, merging to fine, indistinct threads posteriorly, and slightly anastomosing anteriorly before merging to fine, indistinct threads; interstices are narrow and shallow. Periostracum calcified, aragonitic, white. Hinge of lv with anterior lateral tooth well developed, knoblike, in height rising above the cardinal teeth from the plain of the hinge plate; anterior cardinal thin, oblique, joined to thick median cardinal forming an inverted v-shape; posterior cardinal long, ridgelike, separated from the median cardinal by a deep pit. Hinge of rv with paired anterior lateral teeth; anterior cardinal short, moderately thick, parallel to the median cardinal; median cardinal bifid, narrowly triangular; posterior cardinal bifid, elongate, oblique. Pallial line thin. Pallial sinus small, a slight sinuation at the base of the posterior adductor muscle scar. Exterior of shell white to creamy white, sometimes with sparse, obscure, irregularly spaced

Table 1

Dimensions of largest paratypes of *Lioconcha (Sulcilioconcha) caledonensis* in mm.

Valve(s)	Sampling station	Length	Height	Width
1 rv	1103	18.5	17.0	6.6
1 pv	1103	14.1	12.2	8.5
1 pv	1129	18.8	17.3	11.4
1 pv	1117	14.7	12.9	8.7



Figure 1a-c, g-i, d-f.

a-c, g-i. Holotype of *Lioconcha (Sulcilioconcha) caledonensis*, Harte & Lamprell, sp. nov. a. left valve, length 18.5 mm. b. interior of right valve. c. posterior view of conjoined valves, height 16.7 mm, width 11.8 mm. g. interior of left valve. h. right hinge. i. left hinge. d-f. *Lioconcha (Sulcilioconcha) melhartae*, Lamprell Collection. d. left valve, length 20.5 mm. e. interior of right valve. f. posterior view of conjoined valves, height 17.7 mm, width 13.4 mm.

Table 2

Conchological comparison of *Lioconcha (Sulcilioconcha) caledonensis* and *L. (S.) melharteeae*.

Character	<i>L. caledonensis</i>	<i>L. melharteeae</i>
Posterior sculpture	commarginal; threads merge and become indistinct. (Figure 1c)	often not commarginal but oblique; threads anastomose and remain distinct. (Figure 1f)
Color pattern	irregular, faint, sparse, zigzag markings; escutcheon and lunule not colored.	a solid posterior radial; occasional commarginal bands; escutcheon and lunule colored.
Umbones	slightly inflated (Figure 1c)	inflated (Figure 1f)
Posterior shape	slightly more angular	convex
Anterior lateral tooth (right valve)	rises above the cardinal teeth from the hinge plane	lower than the cardinal teeth
Early teleconch	smooth	sculptured

and scaped lines and small triangles; internal color white or cream.

Type material: Holotype: MNHN; Nouvelle-Calédonie, Secteur des Belep: 1 pv, sta. 1103, 32 m, 19°43'S, 163°57'E, white muddy sand with oyster shells. B. Richer-ORSTOM coll. 25 October 1989. Dimensions of holotype: length 18.5 mm, height 16.7 mm, width of conjoined valves 11.8 mm. Paratypes: MNHN; Nouvelle-Calédonie, Secteur des Belep: 2 pv, 2 rv, 1 lv same data as holotype; 7 pv (+ 1 pv Australian Museum Sydney, AMS C312630), sta. 1129, 40 m, 19°29'S, 163°49'E; 5 pv, sta. 1117, 36 m, 19°38'S, 163°54'E; Lagon Nord: 1 pv, sta. 484, 35 m, 19°00'S, 163°35'E; 2 pv, sta. 517, 42 m, 19°09'S, 163°35'E; 4 pv, sta. 522, 42 m, 19°08'S, 163°38'E. For dimensions of some paratypes, see Table 1.

Distribution: Specimens of this species are known only from the Belep Islands of New Caledonia ranging from 12°29'S, 163°49'E to 19°43'S, 163°57'E in depths between 32 and 42 m. Sampling station environments include sta. 1103 (see holotype, above); for sta. 1117, coarse, muddy sand with turritellid shells; and for sta. 1129, white, coarse, shelly sand, with *Amusium*.

Remarks: This species is most similar to *Lioconcha (Sulcilioconcha) melharteeae* Lamprell & Stanisc, 1996. Several conchological characters distinguish *Lioconcha caledonensis* from *L. melharteeae* (Table 2; Figure 1a–f) and the other species within *Sulcilioconcha*. *Lioconcha caledonensis* has flattened ribs with shallower interstices and is often less colored than *L. (S.) philippinarum* (Hanley, 1844) or *L. (S.) amirantium* (Melville, 1909), an Indian Ocean species very similar to *L. philippinarum*; the latter two species have rounded ribs and are often colored brown on the shell, escutcheon, and lunule. *Lioconcha (Sulcilioconcha) richerdeforgesi* Lamprell & Stanisc, 1996, is less trigonal with less inflated umbones, more color patterns and narrower ribs, and generally smaller than *L. caledonensis*. *Lioconcha (Sulcilioconcha) dautzenbergi* (Prashad, 1932) is creamier in col-

or, heavily patterned, and has much wider, rounded ribs. Both *Lioconcha (Sulcilioconcha) trimaculata* (Lamarck, 1818) and *Lioconcha (Sulcilioconcha) polita* (Röding, 1798) are more ovate in shape, and more heavily patterned and colored, with colored lunules and escutcheons, and purple or brown colors internally; *L. polita* is smooth centrally.

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International Commission on Zoological Nomenclature

The following Application was published on 30 September 1998 in Volume 55, Part 3 of the *Bulletin of Zoological Nomenclature*. Comment or advice on this application is invited for publication in the *Bulletin* and should be sent to the Executive secretary, I. C. Z. N., c/o The Natural History Museum, Cromwell Road, London SW7 5BD, U.K. (e-mail: iczn@nhm.ac.uk).

Case 3087—*Hydrobia* Hartmann, 1821 and *Cyclostoma acutem* Draparnaud, 1805 (currently *Hydrobia acuta*; Mollusca, Gastropoda): proposed conservation by replacement of the lectotype of *H. acuta* with a neotype; *Ventrosa* Radoman, 1877: proposed designation of *Turbo ventrosus* Montagu, 1803 as the type species; and HYDROBIINA Mulsant, 1844 (Insecta, Coleoptera): proposed emendation of spelling to HYDROBIUSINA, so removing the homonymy with HYDROBIIDAE Troschel, 1857 (Mollusca).

The following Opinion concerning mollusks was published on 30 September 1998 in Volume 55, Part 3 of the *Bulletin of Zoological Nomenclature*. Copies of this Opinion can be obtained free of charge from the Executive Secretary at the address given above.

Opinion 1905. S. D. Kaicher (1973–1992), *Card Catalogue of World Wide Shells*: not suppressed for nomenclature purposes.

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c) Composite works:

Feder, H. M. 1980. Asteroidea: the sea stars. Pp. 117–135 in R. H. Morris, D. P. Abbott & E. C. Haderlie (eds.), *Intertidal Invertebrates of California*. Stanford University Press: Stanford, Calif.

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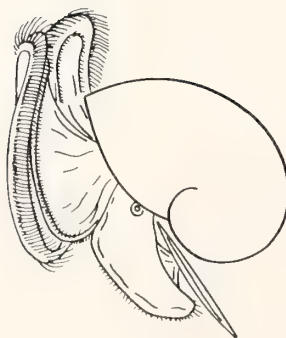
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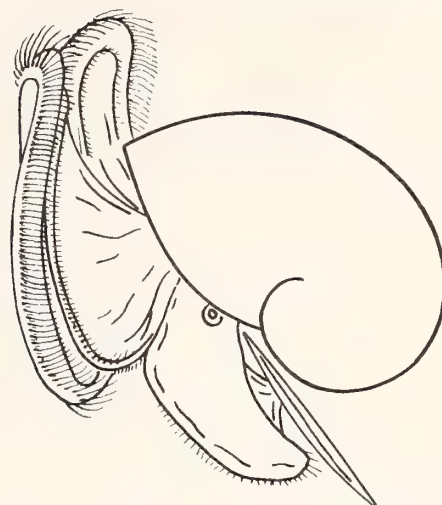
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THE VELIGER

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Utilization of Artificial Diets and Effect of Protein/Energy Relationship on Growth Performance of the Apple Snail *Pomacea bridgesi* (Prosobranchia: Ampullariidae)

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Abstract. Two feeding experiments were conducted with juvenile apple snails (*Pomacea bridgesi*). The first was aimed at determining growth performance and adaptability with a natural vegetable source (dehydrated lettuce, D = 1) compared with a composite diet of high content of fishmeal (D = 2). Snails of three different shell lengths (S1 = 7.5 ± 0.92 , S2 = 12.6 ± 0.29 , and S3 = 19.3 ± 0.46 mm) were fed at two different percentages of total weight (2% and 6%). The best results ($P < 0.05$) in terms of specific growth rate (SGR), shell length increase (SLI), feed conversion rate (FCR), and protein efficiency ratio (PER) were obtained with the artificial feed (D2). Snails of smaller length (S1) exhibited the best growth rate, being thus able to assimilate complex diets beginning from this length. Better results were obtained when snails were fed at 6% of their total weight. In the second experiment, a series of eight semi-purified formulations with varying levels of protein (10–40%) and energy (250–350 kcal/100g feed) were fed to triplicate groups of freshwater apple snails for 28 days. Results indicated that the SGR increased, as well as SLI, FCR, and PER with protein levels ranging from 20% to 30%. Low-energy diets (250 kcal/100g feed) were superior to high-energy diets (350kcal/100g feed) for all levels of protein tested. The SGR, FCR, and PER improved as dietary energy level was raised to 85 mg prot/kcal. Further increase of dietary energy had no beneficial effect in each protein level. Growth rates achieved in both experiments with artificial diets (13.83 and 14.16 mm/month, respectively) are far superior to those regularly obtained under laboratory conditions and even to those observed in the wild. The rapid growth rate attained and the ready acceptance of artificial diets suggest that the species could be cultured under intensive culture conditions.

INTRODUCTION

Apple snails or “tegogolos” (*Pomacea*) are freshwater mollusks quite common in the tropical lowlands of south-eastern Mexico (Rangel, 1988) and the south of North America (Bânărescu, 1990), which present various characteristics that make them suitable for culture. They are herbivorous, thus efficient energy converters; they are prolific, reproducing all year round. They can be handled in combination with other species; such as tilapia (Ontiveros, 1989), tolerate a wide range of environmental conditions, have well-established local markets in some regions of the Caribbean and Mexico (Lum-Kong, 1989; Asiain & Olguín, 1995), and under controlled culture conditions, it is possible to avoid transmission of human diseases and parasites, often related to consumption of wild organisms (Asiain & Olguín, 1995). In addition to this, the genus *Pomacea* appears to possess other desirable qualities, which makes it attractive for culture. The most important feature is the rapid growth rate exhibited by individuals in the wild (13.52 mm/month, attaining a

maximum length of 145 mm), which means more meat weight compared with smaller species of cultured snails (Burky, 1974; Lum-Kong, 1989). Its amphibious nature permits it to inhabit water low in dissolved oxygen and to withstand some crowding, indicating the potential for intensive culturing. Fairly high fecundity, high hatchability, low mortality, short developmental period, and advanced state of hatching also enhance the prospects for culture (Lum-Kong & Kenny, 1989). The fact that the snail can withstand extended periods out of water (Burky, 1973) allows easy transportation to markets, and death as a result of handling is minimal. This results in reduction of labor and transport costs (Lum-Kong, 1989). This genus has also received considerable attention because of its potential as human food (Lum-Kong & Kenny, 1989), source of protein for other aquatic animals (Bombeo-Tuburan et al., 1995), for its role in biological control of aquatic weeds (Cazzaniga, 1981, 1983), and predation on schistosome-bearing gastropods (Cazzaniga, 1990; Estebenet & Cazzaniga, 1992).

Despite all these advantages, the unwise introduction of these snails has had adverse ecologic and economic consequences, and in some cases, these snails have been

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considered as pests in rice paddies because they feed on young rice plants (Bombero-Tuburan et al., 1995; De Silva, 1989).

In the wild, apple snails feed preferentially on macrophytic vegetation (Estebenet, 1995), so under controlled culture conditions they have been traditionally fed with vegetable matter such as lettuce, alfalfa, *Chara vulgaris*, *Potamogeton pectinatus*, *Psidium guajava*, *Pistia stratiotes* (Cazzaniga, 1981; Lum-Kong, 1989; Martinez, 1989; Estebenet & Cazzaniga, 1992). In a general way, this type of food is difficult to store, has variable nutritional quality, and its availability is season-dependent. Therefore, development of a cost-effective practical feed is desirable for mass culture of the apple snail. At present, despite some major contributions on different aspects of gastropod digestive anatomy (Andrews, 1965), digestive physiology (Vonk & Western, 1984), and nutrition (Carefoot, 1982), knowledge of the quantitative and qualitative food requirements of the genus *Pomacea* has yet to be achieved. The production of a specific aquatic organism can be economical only when these requirements are known. Moreover, most of the experimental diets tested are commercial diets formulated to meet the requirements of other species (Estebenet & Cazzaniga, 1992; Benavides, 1994).

A major obstacle in formulating a complete diet is the lack of information of the specific nutrient requirements of these animals, particularly the utilization of macronutrients such as protein, carbohydrates, and lipids. Considering that protein is the most expensive component of prepared feeds, several studies have shown that an adequate energy supply with non-protein energy sources can minimize its use, whereas an excess of energy may reduce total protein intake, as has been shown in other cultured species like shrimp (Shiau & Chou, 1991). Therefore, the critical point is to obtain the proper protein/energy (P/E) ratio in a diet for the most economical production of the apple snail. Reduction of protein in the diet would also reduce the amount of ammonia being excreted. Until now, only some attempts have been made to rear apple snails on artificial pellet diets (Benavides, 1994); a formulation which promotes optimal growth in these animals has not yet been reported.

Since P/E relationships are basic to defining other nutritional requirements (Andrews et al., 1972), the present study was conducted to gain preliminary information on growth response to various levels of dietary proteins by the apple snail.

MATERIALS AND METHODS

Two feeding experiments were conducted with juvenile apple snails (*Pomacea bridgesi* Reeve, 1856). The first experiment was designed to test the growth performance and adaptability of a natural vegetable source (dehydrated lettuce) compared with an artificial diet containing a high

percentage of fishmeal. Individuals of three different lengths were fed at two percentages of the total weight of the snails in each aquarium, respectively.

In the second experiment, eight semi-purified diets (Lovell, 1980) were used to establish the quantitative P/E requirements of the snails. Four protein and two energy levels were fed to triplicate groups of freshwater apple snails.

Experimental Animals

A batch of apple snails was originally obtained from a local aquarium store in 1993 and maintained and reproduced in captivity. At the start of the growth trials, 30 uniform-sized juvenile snails were selected and allotted at random in three glass aquaria. The experimental diets were fed to triplicate groups of 10 juvenile apple snails stocked in 31.25 L glass aquaria. The length of the shells (from the apex of the shell to the basal extreme aperture) was measured with a caliper to the nearest 0.1 mm. In the first experiment, the snails were sorted in three different length classes ($S1 = 7.5 \pm 0.92$, $S2 = 12.6 \pm 0.29$, and $S3 = 19.3 \pm 0.46$ mm) and each group was fed at 2% and 6% of the total weight of the snails of each aquarium, respectively with two different diets: Diet 1 = dehydrated lettuce and Diet 2 = artificial diet for 28 days. As 30 snails were used per treatment, a total of 360 snails was to cover the combination of the above mentioned treatments ($3 \times 2 \times 2$).

For the second experiment, a different batch of snails of one length only was used. They had an average individual length of $16.3 \text{ mm} \pm 2.3 \text{ mm}$ and a mean weight of $1.27 \text{ g} \pm 0.52 \text{ g}$. A total of 280 snails was randomly divided into eight groups, and fed different diets in triplicate containing four protein (10, 20, 30, and 40%) and two energy levels (250 and 350 kcal/100g feed), respectively, for 28 days. Each group was fed twice a day at a rate of 4% of the total weight of the snails in each aquarium daily.

In both experiments, the snails were acclimated to laboratory conditions for 1 week in a 1500 L fiberglass tank ($2.50 \times 1.50 \times 0.4 \text{ m}$; $L \times W \times H$). During this period, the snails received fresh lettuce as a maintenance diet.

Composition of the Experimental Diets

Ingredients, chemical composition, and the P/E content of the experimental diets are summarized in Tables 1, 2, and 3, respectively. Proximate analysis of diets was conducted by standard Association of Official Analytical Chemists (AOAC) methods (AOAC, 1984). Moisture was determined gravimetrically considering thermic elimination of water (by drying at 105°C), crude protein by a microKjeldahl method. Crude lipids were either extracted by the Soxhlet method; crude fiber was obtained in a fat-free material sample by dilute acid and alkali treatment; ash content was determined in a muffle furnace by heat-

Table 1

Ingredients used for the formulation of the artificial diet (D1) tested in experiment 1.

Ingredients	g/100 g dry diet
Fish meal	30.00
Soybean meal	5.60
Wheat meal	47.85
Shrimp meal	4.00
Wheat gluten	5.00
Fish oil	3.00
Lecithin	1.70
Vitamin mix ^a	2.50

^a Vitamin mix (mg/kg dry diet): thiamin 150, riboflavin 100, pyridoxine 50, pantothenic acid 0.1, niacin 300, biotin 1, B12 100, folic acid 0.1, vitamin E 400, vitamin K 20, vitamin A 15,000 IU/kg, vitamin D 7500 IU/kg.

ing at 550°C for 3 h; and nitrogen free extract (NFE) was calculated by difference ($NFE = 100 - \text{moisture} + \text{protein} + \text{lipid} + \text{ash}$).

In semi-purified diets the energy levels were adjusted by varying the ratio of dextrin to cellulose; lipid level was kept constant at 25 g/kg of the diet. Since digestible energy values of foodstuffs for apple snails are unknown, physiological values for other invertebrates (Shiu & Chou, 1991) were taken into account for calculation of the energy level (5 kcal/g protein, 9 kcal/g lipids, and 4 kcal/g carbohydrates).

Feeds and Feeding

Feed ingredients were ground, sieved, and mixed. The mixture was pelleted with a meat grinder equipped with a 1.5 mm die. Pelleted diets were dried at 80°C for 1 hr, placed in plastic bags, stored at -20°C, and a 2-day supply was transferred to a refrigerator as needed.

In experiment 1, fishmeal was used as the main protein source (Table 1). In the second experiment, only casein was used as protein source (Table 3). In the latter case, the protein content was adjusted by varying the amount of casein. The daily ration was given in two equal portions at 08:00 and 16:00 hr, and each morning before feeding, feces and other detritus in each aquarium were siphoned out and mortality was recorded.

Experimental Facilities

Snails for growth studies were placed in 31.25 L glass aquaria (50 × 25 × 25 cm) filled up to 25 L. The aquaria were provided with aeration and furnished with filtered dechlorinated hard tap freshwater. Two-thirds of the water in the aquaria was exchanged daily to remove impurities and maintain water quality. The dissolved oxygen level was kept at least at 6.0 ppm throughout the experimental period. Water temperature was maintained in the aquaria

Table 2

Chemical composition of the diets (D1 and D2) tested in experiment 1.

	Dehydrated lettuce	Commercial feed
Protein	15.35	34.83
Ether extract	2.22	3.89
Crude fiber	12.91	2.25
Ash	11.34	9.09
N-free extract	58.18	49.94
CME (kcal/100 g) ^a	292.45	408.92
P/E ratio (mg prot/kcal)	45.45	85.4

^a CME: Calculated metabolizable energy (kcal/g) based on protein, 5 kcal/g; fat, 9 Kcal/g; carbohydrate, 4 kcal/g (Shiau & Chou, 1991).

by means of electric heaters, and ranged from 26–28°C during this period. Continuous aeration was provided in each tank throughout the experiment by an air compressor. The pH of the water varied between 8.0 and 8.2. Both experiments were conducted on a 12 hr light/dark photoperiod cycle.

Growth Trial

Following a fasting period of 24 hr, the animals were individually weighed and measured to register the initial weight and length. After this, they were weighed in bulk on the 7th and 14th day to adjust feed allowances. At the end of the study, animals were taken from each tank and were again individually weighed and measured. The animals were blotted dry before being weighed on a Sartorius balance to the nearest 0.01 g.

Calculation of Snail Performance

Specific growth rate (SGR) = $100 (\ln \text{ average final weight} - \ln \text{ average initial weight}) / \text{No. of days}$, Shell length increase (SLI) = average final length - average, initial length, Feed conversion rate (FCR) = dry weight feed (g)/wet weight gain (g), Protein efficiency ratio (PER) = weight gain (g)/protein fed (g), and Survival = number of individuals at the end of the experiment/number of individuals at the beginning of the experiment × 100, were determined at the end of the experiment.

Statistical Analysis

The growth differences among the snails reared on the various diets were analyzed in the first experiment by a factorial ANOVA (3 × 2 × 2) with three replicates per treatment combination, while for the second experiment data were subjected to a bifactorial ANOVA (4 × 2). The New Duncan multiple range test (Steel & Torrie, 1980)

Table 3
Protein and energy content of diets used in the second experiment.

Ingredients g/100 g dry diet	D1	D2	D3	D4	D5	D6	D7	D8
CME (kcal/100 g) ^a	250				350			
Protein (%)	10.00	20.00	30.00	40.00	10.00	20.00	30.00	40.00
Casein	11.10	22.20	33.30	44.40	11.10	22.20	33.30	44.40
Dextrin	43.30	30.80	18.30	5.80	68.30	55.80	43.30	30.80
Fish oil	2.50	2.50	2.50	2.50	2.50	2.50	2.50	2.50
Cellulose	27.10	28.50	29.90	31.30	2.10	3.50	4.90	6.30
Agar	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.00
Carragenin	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00
Maltose	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Vitamin mixture ^b	5.00	5.00	5.00	5.00	5.00	5.00	5.00	5.00
Mineral mixture ^c	5.00	5.00	5.00	5.00	5.00	5.00	5.00	5.00
P/E (mg prot/kcal)	40.00	80.00	120.00	160.00	28.50	57.10	85.70	114.00

^a CME: Calculated metabolizable energy (kcal/g) based on protein, 5 kcal/g; fat, 9 Kcal/g; carbohydrate, 4 kcal/g (Shiau & Chou, 1991).

^b Vitamin mix (mg/kg dry diet): thiamin 300, riboflavin 200, pyridoxine 100, pantothenic acid 0.21, niacin 600, biotin 2, B12 200, folic acid 0.2, vitamin E 800, vitamin K 40, vitamin A 30,000 IU/kg, vitamin D 15,000 IU/kg.

was used to identify differences among means at 0.05 level.

RESULTS

Growth performance of snails fed the experimental diets is presented in Tables 4 and 5 and in Figures 1 to 8.

Experiment 1:

Specific growth rate. SGR was the variable that reflected the best the effect of the different factors considered (type of feed, feeding level, and initial shell length) as Figure

1 shows. Significant differences ($P < 0.05$) were observed for every interaction of these factors (Table 4).

Shell Length Increase. No significant differences were detected for this variable when the initial length of snails was compared, or when the interaction between initial length and type of feed was considered. Significant differences ($P < 0.05$) were registered only when the kind of feed and the feeding level were considered together. The better performance of both diets when supplied at 6% of the total weight and the marked difference between the artificial diet and the dehydrated lettuce are notable.

Table 4

Specific growth rate (SGR), shell length increase (SLI), feed conversion ratio (FCR), and protein efficiency ratio (PER) for the experimental diets of the first experiment 1.

Diet	Feed supply	Length (mm)	SGR ¹	SLI ²	FCR ³	PER ⁴
Dehydrated Lettuce	2%	7.50	2.31 ± 0.55 ^e	1.90 ± 0.69 ^d	1.19 ± 0.31 ^{bc}	5.85 ± 1.59 ^{abc}
		12.60	0.82 ± 0.22 ^b	1.33 ± 0.41 ^d	2.45 ± 0.58 ^e	2.83 ± 0.75 ^e
		19.30	0.91 ± 0.36 ^b	1.76 ± 0.11 ^d	2.26 ± 0.98 ^{de}	3.33 ± 1.30 ^{de}
	6%	7.50	4.71 ± 0.08 ^{de}	5.86 ± 0.72 ^c	1.58 ± 0.04 ^{cd}	4.18 ± 0.11 ^{cde}
		12.60	3.72 ± 0.18 ^f	6.63 ± 0.15 ^{bc}	0.98 ± 0.11 ^{abc}	7.27 ± 0.40 ^{ab}
		19.30	2.16 ± 0.53 ^e	5.46 ± 2.07 ^c	2.70 ± 0.71 ^e	2.60 ± 0.63 ^e
Commercial Feed	2%	7.50	5.77 ± 1.36 ^c	5.56 ± 1.30 ^c	0.39 ± 0.15 ^a	8.18 ± 3.70 ^a
		12.60	3.86 ± 0.53 ^{ef}	7.00 ± 0.36 ^{bc}	0.49 ± 0.06 ^{ab}	5.83 ± 0.80 ^{abc}
		19.30	3.58 ± 0.13 ^f	7.90 ± 0.95 ^b	0.48 ± 0.01 ^{ab}	5.80 ± 0.43 ^{abc}
	6%	7.50	9.49 ± 0.23 ^a	13.83 ± 0.61 ^a	0.70 ± 0.05 ^{ab}	3.98 ± 0.24 ^{cde}
		12.60	6.90 ± 0.50 ^b	12.91 ± 1.10 ^a	0.52 ± 0.04 ^{ab}	5.40 ± 0.42 ^{bcd}
		19.30	5.27 ± 0.29 ^{cd}	12.30 ± 0.70 ^a	0.97 ± 0.04 ^{abc}	2.93 ± 0.14 ^e

¹ Figures with different superscripts in the same column are significantly different from each other ($P < 0.05$); means of triplicate groups ± SD.

Table 5

Specific growth rate (SGR), shell length increase (SLI), feed conversion ratio (FCR), and protein efficiency ratio (PER) for the eight semi-purified experimental diets of the second experiment 1.

CME (kcal/100 g)	Protein (%)	P/E (mg prot/kcal)	SGR ¹	SLI ²	FCR ³	PER ⁴
250	10.00	40.00	4.02 ± 0.06 ^{cd}	9.66 ± 0.49 ^c	0.90 ± 0.04 ^c	11.02 ± 0.49 ^a
	20.00	80.00	5.39 ± 0.35 ^{ab}	14.0 ± 0.1 ^a	0.60 ± 0.05 ^a	8.28 ± 0.77 ^b
	30.00	120.00	5.51 ± 0.37 ^{ab}	12.96 ± 0.68 ^{ab}	0.63 ± 0.06 ^a	5.31 ± 0.57 ^d
	40.00	160.00	4.82 ± 0.3 ^b	11.3 ± 1.3 ^{bc}	0.56 ± 0.03 ^a	4.43 ± 0.31 ^{de}
350	10.00	28.50	3.6 ± 0.23 ^d	7.86 ± 0.66 ^d	1.08 ± 0.04 ^d	9.2 ± 0.36 ^b
	20.00	57.10	4.72 ± 0.26 ^{bc}	11.76 ± 0.2 ^b	0.77 ± 0.04 ^b	6.44 ± 0.38 ^c
	30.00	85.70	5.77 ± 0.6 ^a	14.16 ± 1.3 ^a	0.63 ± 0.1 ^a	5.31 ± 0.94 ^d
	40.00	114.00	5.49 ± 0.72 ^{abc}	12.93 ± 1.7 ^{ab}	0.66 ± 0.1 ^{ab}	3.85 ± 0.55 ^e

¹ Figures with different superscripts in the same column are significantly different from each other ($P < 0.05$); means of triplicate groups ± SD.

Feed Conversion Rate. The FCR did not seem to be affected by the feeding level or by the initial weight of the animals. Nevertheless, there is a slight tendency of smaller animals to show a better FCR. Significant differences ($P < 0.05$)

were only observed for the source of protein and for the lower FCR obtained with the artificial diet.

Protein Efficiency Ratio. No clear tendency for this factor

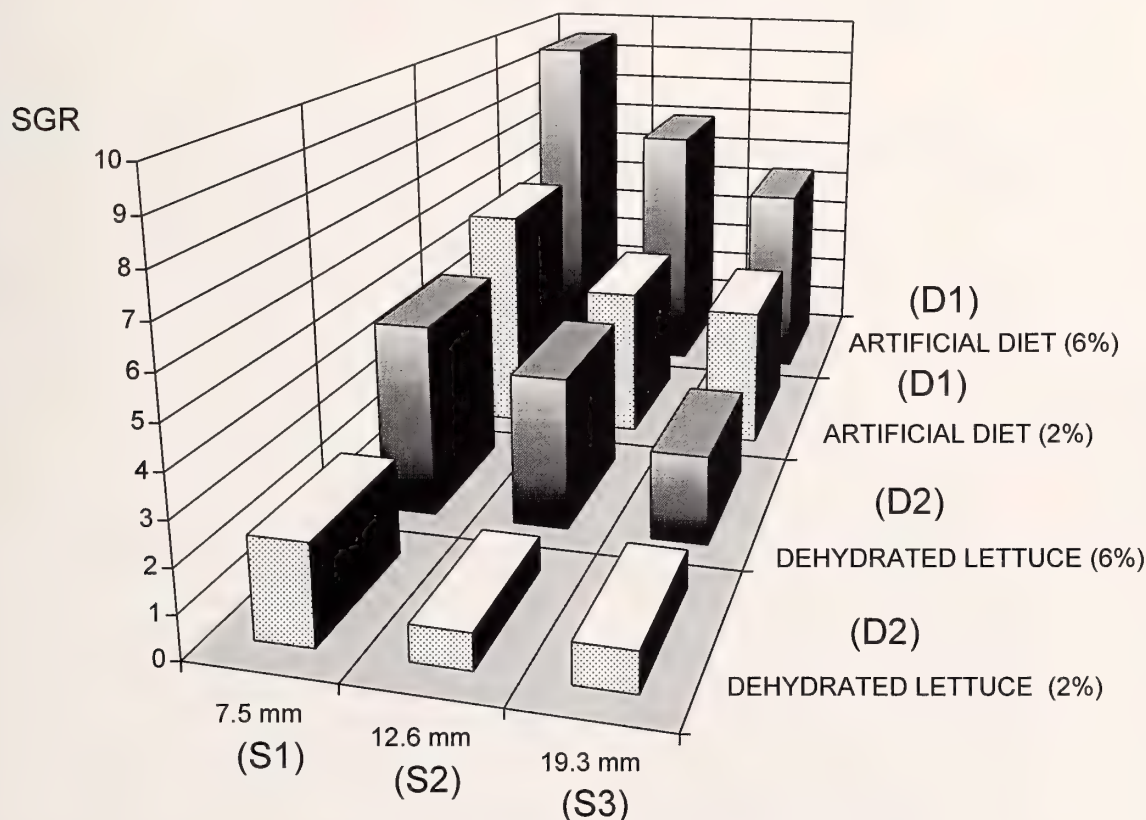


Figure 1

Specific growth rate of *Pomacea bridgesi* juveniles of three different lengths fed with an artificial and natural diet supplied at two daily rations.

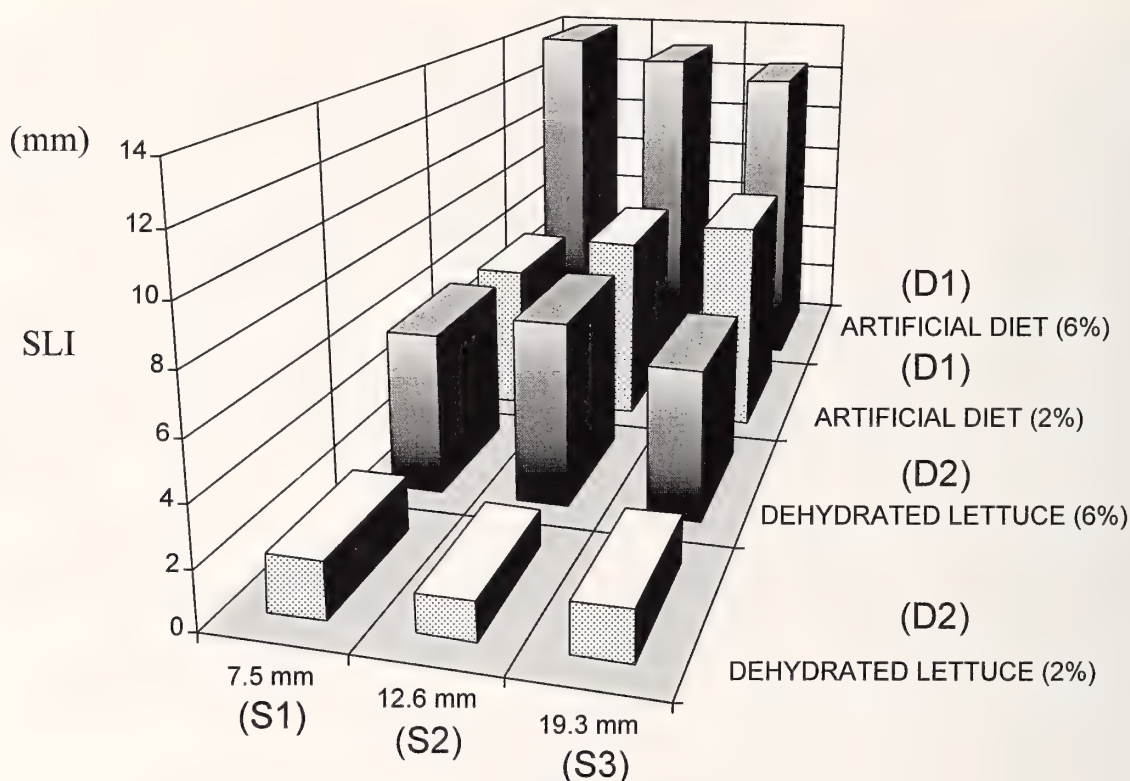


Figure 2

Shell length increase of *Pomacea bridgesi* juveniles of three different lengths fed with an artificial and natural diet supplied at two daily rations.

was observed, except that the higher values obtained for the smaller animals fed the diets containing animal protein stand out.

Experiment 2:

Specific growth rate. Significant differences were found with regard to the protein level. The best performance was obtained with levels ranging from 20–40% ($P < 0.05$) (Table 5). In this table it is also evident that growth rate increases proportionally with the P/E ratio up to a level of 85 mg protein/kcal after which it decreases slightly.

Shell length increase. Results were similar to those observed for SGR. Higher values were obtained with P/E ratios ranging from 80 to 85 mg protein/kcal ($P < 0.05$).

Feed conversion rate. As for the other variables the best results were obtained with protein levels higher than 10% with the best values in terms of P/E starting from 80 mg protein/kcal up to 160 mg protein/kcal ($P < 0.05$).

Protein efficiency ratio. A clear tendency, although not significant, was observed concerning the protein level. On

the other hand, it was observed that the PER decreased simultaneously with the P/E ratio.

Survival. The mortality rate was less than 1% for both experiments (0.8% in the first and 0.4% in the second).

DISCUSSION

The best results in terms of SGR and SLI were obtained with the feed containing animal protein. In spite of the absence of significant differences regarding the length of snails, those of smaller length (7.5 mm) showed the best performance for the growth rate (Table 4, Figures 1, 2). Calcium was unlikely to be limiting, as hard tap water was used for experiments. On the other hand, soft body parts seem to reflect more clearly the nutritional state of gastropods (Brendelberger, 1995). The fact that the smaller snails showed a better growth rate is explained by their better FCR and PER, which would mean that even at this length they are able to assimilate complex diets. The better performance of artificial feed compared with lettuce can also be appreciated by the results of FCR and PER (Figures 3, 4). This may imply a better digestion of the composite diet, but it is also possible that the lettuce was

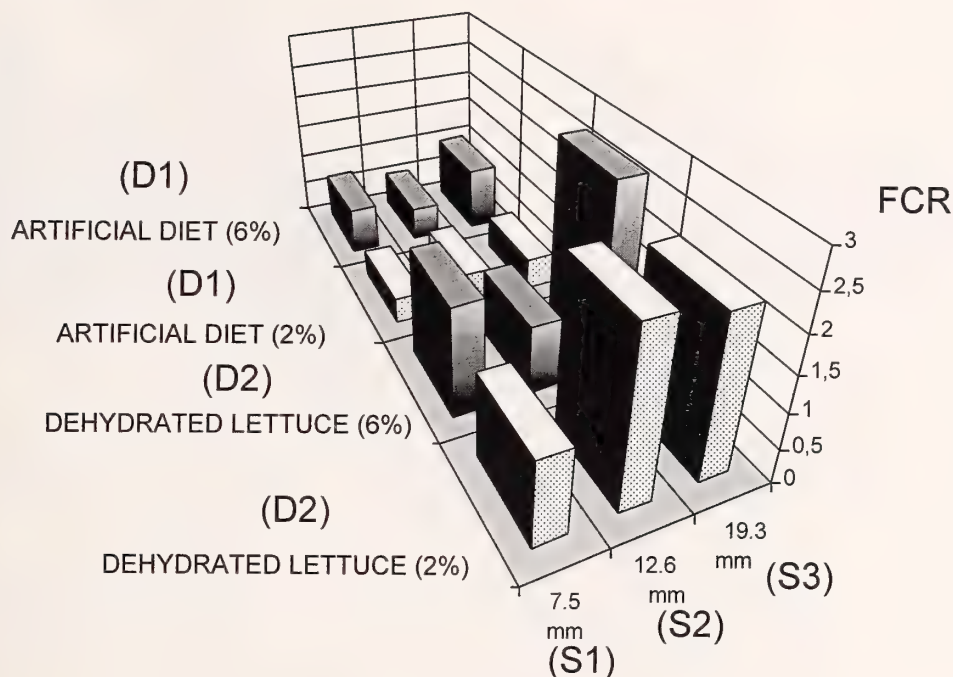


Figure 3

Feed conversion ratio of *Pomacea bridgesi* juveniles of three different lengths fed with an artificial and natural diet supplied at two daily rations.

not as actively consumed by the snails as the artificial diet because of poor palatability. It has been reported for other invertebrates that diets containing a mixture of two or more proteins are better utilized (Alava & Lim, 1983). It was noted that when both diets were supplied at 6% of the total weight, the PER decreased, possibly because the quantity of protein exceeded the digestive capacity of the snails and also because of a higher energetic expenditure to excrete the excess protein. The results obtained in this study are not in agreement with those reported by Estebenet & Cazzaniga (1992) who found a better growth rate in newly hatched snails reared on fresh lettuce than in those with composite diets. However, the lack of data regarding the protein content of the different diets tested and the FCR make it difficult to interpret their results.

Lettuce was employed as a reference diet, because it has been used in most of the feeding bioassays with snails of the genus *Pomacea* (Meenakshi, et al., 1975; Martinez, 1989; Estebenet & Cazzaniga, 1992). Artificial diets were developed as an alternative to the difficulty of harvesting large quantities of aquatic plants, traditionally considered as important for freshwater snails, together with the high storage costs, (Estebenet, 1995). In relation to this, artificial diets have proved effective for the culture and maintenance of other prosobranchians (*Biomphalaria glabrata*, Standen, 1951; *Marisa cornuarietis*, Ferguson, 1978), and have also given good results in terms of growth and food conversion rate with other gastropods such as aba-

lone (McVeigh, 1994). It was necessary to know the appropriate feeding rate for the apple snail because no data were available in the literature. Indeed, in most of the feeding studies carried out with individuals of the genus *Pomacea*, the animals have been fed *ad libitum* (Cazzaniga & Estebenet, 1988; Lum-Kong, 1989; Martinez, 1989; Ontiveros, 1989; Asiain & Olguín, 1995). The eventual differences in feed consumption may mask the performance of the diet, as was observed in the first experiment where similar growth rates were obtained when animals were fed at 2% of the total weight with an artificial diet or at 6% with the dehydrated lettuce (Figures 1, 2). Similarly, Cazzaniga (1981) and Estebenet (1995) found out that a 6.0 g snail could consume from 4.9 to 12.5 g/day of vegetable matter (with a protein content varying from 0.9 g to 0.18 g), depending on the aquatic plant attractiveness and palatability. This would be equivalent to feeding the snails with only 0.3 g to 0.6 g of an artificial feed formulated to have 30% protein. Other results demonstrated that the feeding level did not have a marked influence on the FCR and the PER (Figures 3, 4); this may be because these variables are determined mostly by the quality and not the quantity of protein, i.e., protein from vegetal or animal sources. This led us to consider that the snail can utilize the artificial diet more effectively than the lettuce. This is in agreement with the data reported by Ontiveros (1989) who observed good growth performance when the snails were fed with fish-

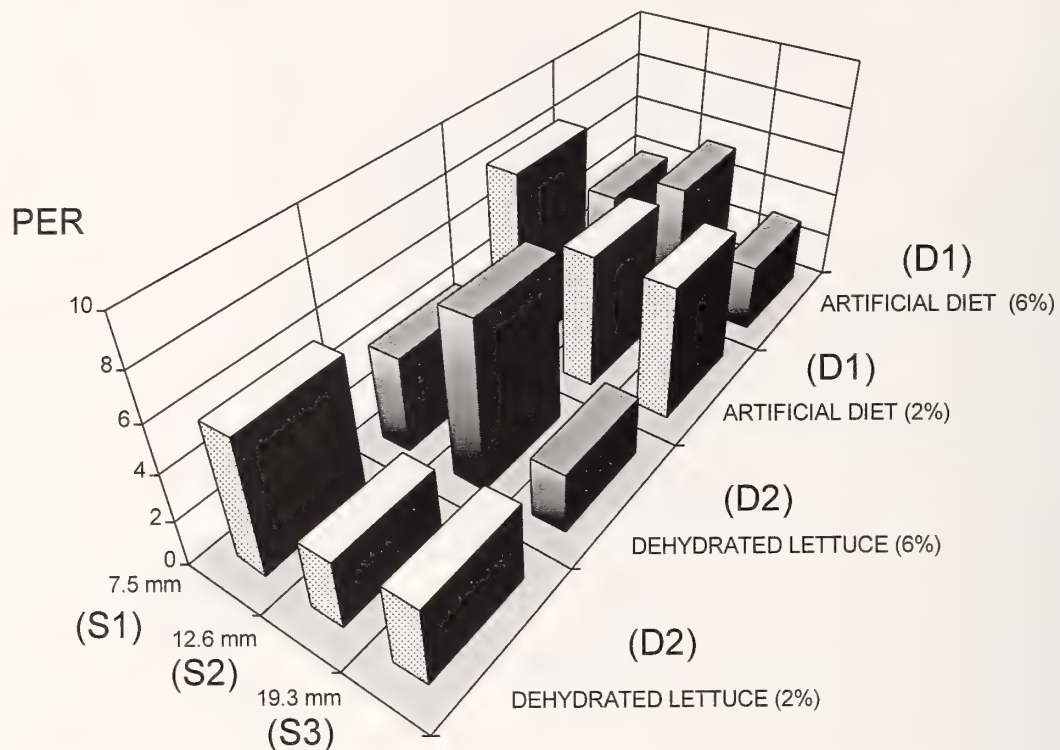


Figure 4

Protein efficiency ratio of *Pomacea bridgesi* juveniles of three different lengths fed with an artificial and natural diet supplied at two daily rations.

meal. Besides, the acceptance of the composite diet containing animal protein is supported by the fact that in the wild they eventually fed on other animals. Indeed, unlike the majority of the freshwater snails which are microphagous, apple snails belonging to the Ampullaridae family show three feeding types (not mutually exclusive): microphagous, zoophagous, and macrophytophagous

(Cazzaniga & Estebebet, 1984); and even if the macrophagous type is most common in *Pomacea*, feeding preferentially on macrophytic vegetation (Cazzaniga, 1987; Estebebet, 1995), it has been reported that under laboratory conditions *Pomacea canaliculata* ate dead animals even when plant material was available, and that *P. paludosa* was able to depredate fish (Cazzaniga & Estebebet,

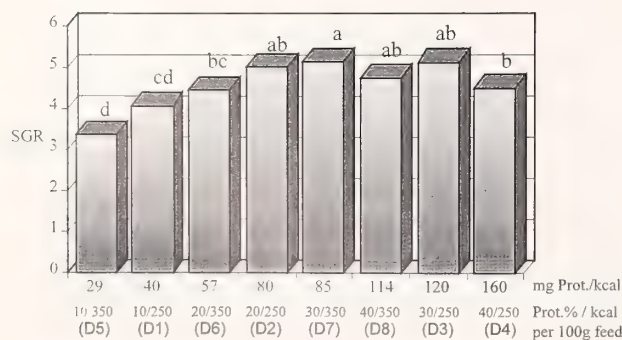


Figure 5

Specific growth rate of *Pomacea bridgesi* juveniles fed diets with different protein/energy ratio for 28 days. Bars with the same superscript are not significantly different ($P < 0.05$).

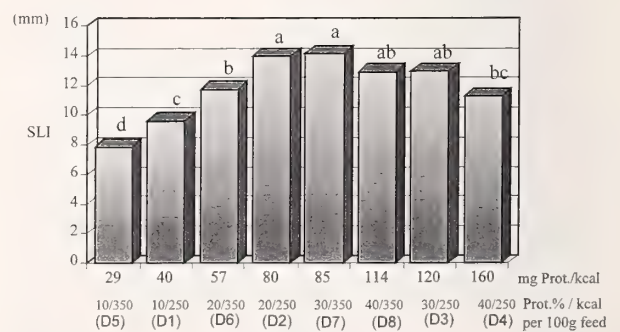


Figure 6

Shell length increase of *Pomacea bridgesi* juveniles fed diets with different protein/energy ratio for 28 days. Bars with the same superscript are not significantly different ($P < 0.05$).

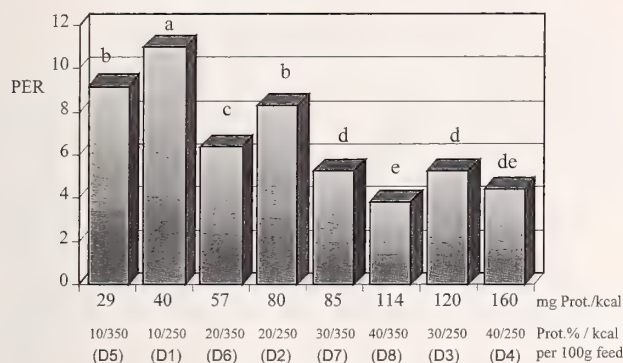


Figure 7

Feed conversion ratio of *Pomacea bridgesi* juveniles fed diets with different protein/energy ratio for 28 days. Bars with the same superscript are not significantly different ($P < 0.05$).

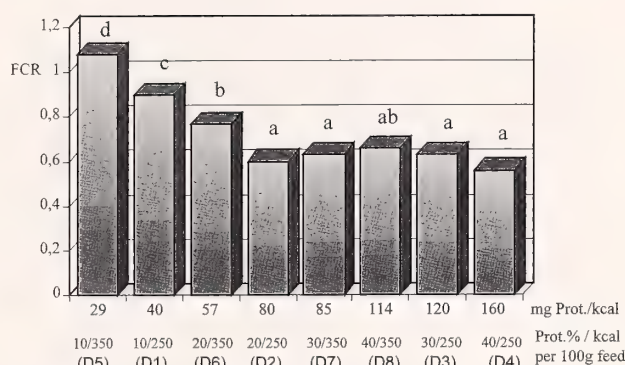


Figure 8

Protein efficiency ratio of *Pomacea bridgesi* juveniles fed diets with different protein/energy ratio for 28 days. Bars with the same superscript are not significantly different ($P < 0.05$).

1984). The same authors indicate that *P. insularum* fed on dying or dead fish. Other ampullarids, like *Marisa cornuarietis*, are capable of eating meat from frogs, fish, and crabs (Ferguson, 1978).

In terms of energy utilization, overall results showed that the best growth performance and shell length increase were obtained with protein levels ranging from 20–30%. When the semi-purified diets are analyzed individually, it can be observed that for those diets with 10% and 20% protein, the energy level of 250 kcal/100g feed resulted in a better growth performance than for diets designed to have 350 kcal/100g feed. On the contrary, this relationship is reversed for diets containing 30% and 40% protein, which showed better results with higher energy levels (350 kcal/100g feed) (Figures 5, 6). This reflects a higher need of energy for a higher protein level. This aspect is also evident when the results of PER and FCR are considered, which indicate that energy levels of 250 kcal/100g feed are better than those of 350 kcal/100g feed for all protein levels and especially for those of 10% and 20% (Figures 7, 8), meaning that the energy content could be limiting the feed ingestion. Indeed, a lack of protein (e.g., 10%), regardless of the energy level, would mean less amino acids available for protein synthesis and deposition, while an excess of protein would imply a higher energetic expenditure for its catabolism and high levels of ammonia excreted, thus being detrimental for intensive culture conditions. In addition, protein would be used for energy and not for growth when inadequate energy is fed (Catacutan & Colosso, 1995); thus, balance of P/E in the feed is important. Considering that there is but a slight difference in growth produced with those diets containing 20% and 30%, the better PER of the former and a similar FCR for both, the protein requirement of *Pomacea bridgesi* appears to be near 20%. When considering the P/E ratio, it is observed that the best performance in terms of SGR, SLI, and FCR was obtained with

values between 80 mg and 85 mg protein/kcal (Figures 6, 7 & 8). This value is close to the optimum reported for other aquatic organisms (88–90 mg protein/kcal, Haiqing & Xiqin, 1994; 83 mg protein/kcal, Xiqin et al., 1993²). The foregoing could explain the difference in growth performance observed for the artificial diet and the dehydrated lettuce in the first experiment—first, by the higher content of protein of the former and second by its energy content. Indeed, it can be appreciated that the P/E ratio of the artificial diet was of 85.40 mg of protein/kcal compared to 45.45 mg protein/kcal for the lettuce. And as can be observed in the second bioassay, in spite of the narrow range of P/E ratio employed in this study, a P/E ratio of 85 mg protein/kcal appears to be the optimum for apple snail juveniles. It should be pointed out that the high fiber content of the lettuce could have resulted in a faster digestive transit and therefore a lower digestibility.

The length achieved in these experiments, 13.83 mm/month in the first experiment and 14.16 mm/month in the second experiment (Figures 2, 6), is far superior to those obtained by other authors under laboratory conditions, as is reflected in the work of Martinez (1989) who reported 5.5 mm/month with *P. patula* fed with alfalfa; Ontiveros (1989) obtained 5.3 mm/month with *P. flagellata* fed with *Pistia* sp., and Benavides (1994) 7.0 mm/month with *Pomacea bridgesi* with a 30% protein fish feed. Our results suggest that the diets used by this author, besides being higher in protein, also had a high energy level (330 kcal/100g feed) and a P/E ratio (90.9 mg protein/kcal), higher than the optimum found in this study. Finally, the results

² Xiqin, H., J. Lizhu, Y. Yunxia & X. Ghohuan. 1993. Studies on the utilization of carbohydrate-rich ingredients and optimal protein: energy ratio in Chinese bream, *Megalobrama amblycephala* Yih. Paper presented at the Fifth Asian Fish Nutrition Network Workshop, Thailand.

obtained are even better than those observed in the wild by Lum-Kong (1989) who registered a shell length increase of 13.5 mm/month for *Pomacea urceus*. This author attributes lower growth rates exhibited by snails in the laboratory to an inadequate diet and high stocking densities.

The importance of this study has been centered on the reduction of the protein level, and one way to spare dietary protein is the utilization of non-protein energy sources, resulting in a reduction of feed cost (Haiqing & Xiqin, 1994).

The rapid growth rates observed in this study suggest that the species can be reared in intensive culture systems. However, before apple snails can be intensively cultured, research is required in the production of artificial diets, optimal stocking densities, and in determining other factors limiting growth under artificial conditions as has been pointed out by Lum-Kong (1989). Study concerning the elaboration of practical diets directed to the development of techniques of intensive culture would lead to the reduction of costs and time involved in manual collection from the wild and subsequent transport (Cazzaniga & Estebenet, 1985).

ACKNOWLEDGMENTS

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A New Species of *Depressigyra*? (Gastropoda: Peltospiridae) from Cold-Seep Carbonates in Eocene and Oligocene Rocks of Western Washington

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Abstract. Continued study of chemosynthetic marine-invertebrate faunas preserved in carbonates formed by the oxidation of methane at ancient cold-seeps reveals, tentatively, the first fossil record of the gastropod family Peltospiridae and the genus *Depressigyra*. *Depressigyra? statura* sp. nov., was found in three cold-seep carbonates within bathyal marine strata in western Washington: the middle Eocene Humptulips Formation; the early Oligocene part of the Makah Formation; and the late Oligocene part of the Lincoln Creek Formation.

INTRODUCTION

Taxonomic work on minute (< 5 mm height) gastropods from modern chemosynthetic communities such as those found near hydrothermal vents and cold seeps is resulting in the recognition of many new families, genera, and species (e.g., McLean, 1989; Warén & Bouchet, 1989, 1993). One recently described gastropod, *Depressigyra globulus* Warén & Bouchet, 1989, is the only known living species of the genus (Warén & Bouchet, 1993). It is one of the most common gastropods in chemosynthetic environments near hydrothermal vents along the Juan de Fuca Ridge (Warén & Bouchet, 1989). Fossils of a new species tentatively referable to the genus *Depressigyra* have been found in localized, methane-derived carbonates within bathyal siltstones in three different formations in western Washington (Figure 1). This is the first detailed study of a minute archaeogastropod from fossil chemosynthetic communities.

The abbreviation used for localities and specimens is LACMIP = Natural History Museum of Los Angeles County, Invertebrate Paleontology Section.

Paleoenvironments

The fauna preserved in a carbonate within the middle to late Eocene Humptulips Formation (LACMIP loc. 12385) was recognized as a chemosynthetic cold-seep community by Goedert & Squires (1990) and Campbell & Bottjer (1993). Benthic foraminifera indicate bathyal depths of 1500 to 2000 m (W. W. Rau cited in Goedert & Kaler, 1996). Carbonate blocks (LACMIP locs. 8233 and 15911) within bathyal basin-plain turbidites of the early Oligocene part of the Makah Formation are allo-

chthonous (Goedert & Campbell, 1995), but they are methane-derived and contain chemosynthetic taxa. This carbonate was precipitated at cold-seeps in a shelf or slope environment, and then broke into blocks up to 2.5 m across when it slid or slumped into deeper parts of a basin (Goedert & Campbell, 1995). A cold-seep carbonate (LACMIP loc. 16504) from the late Oligocene part of the Lincoln Creek Formation was first reported by Squires (1995); it contains a diverse chemosynthetic assemblage that is absent in the surrounding bathyal siltstone (Squires & Goedert, 1995; Rigby & Goedert, 1996).

All of these carbonates differ from other "normal" deep-water carbonates (e.g., nodules and concretions), in that they contain fossils of large numbers of organisms that are not present in surrounding strata, calcite and/or quartz lined vugs, and wavy-laminated carbonate crusts. These deep-water carbonates formed due to the bacterial oxidation of methane at cold-seeps. This interpretation was based on sedimentologic and paleontologic evidence (Campbell & Bottjer, 1993; Goedert & Squires, 1990; Rigby & Goedert, 1996; Squires, 1995; Squires & Goedert, 1991, 1995). The faunas contained in these distinctive carbonates and their depositional context compare well with western North American ancient and modern cold-seep carbonates described by Campbell & Bottjer (1993), Campbell et al. (1993), and Kulm & Suess (1990).

The new species of *Depressigyra?* is abundant and well preserved in both the Humptulips Formation and the Lincoln Creek Formation carbonates. Few specimens were found in the Makah Formation; however, most of the shell was lost during preparation because of the indurated nature of the micrite.

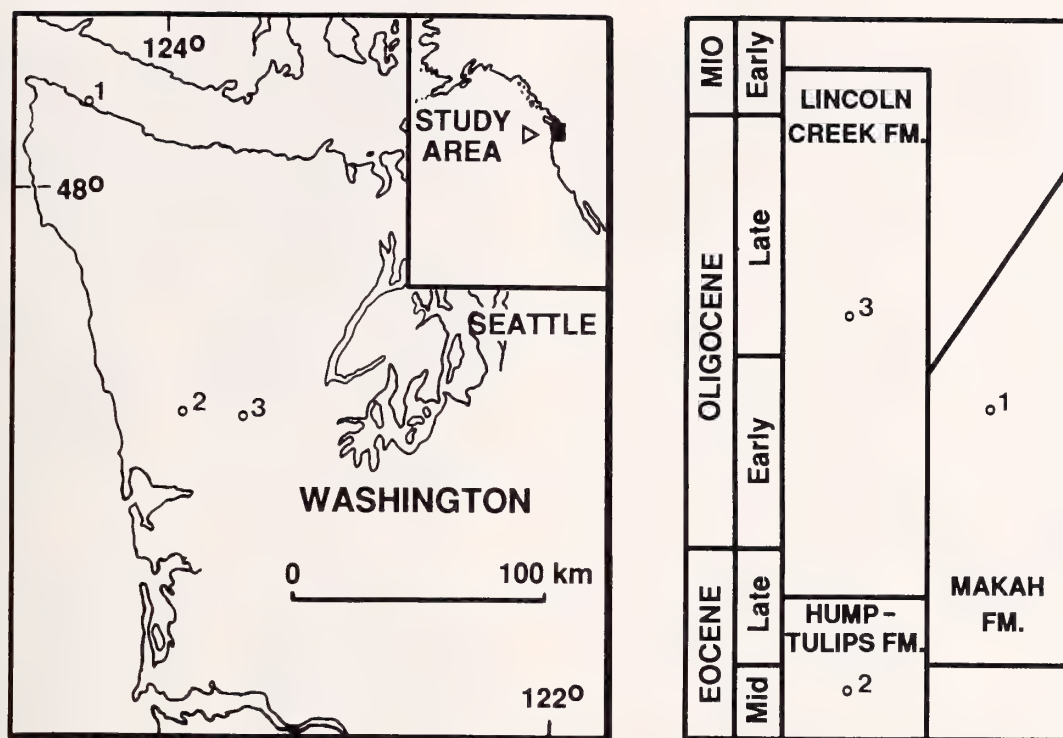


Figure 1

Generalized geographic and chronostratigraphic distribution of localities for *Depressigyræ? statura* Goedert & Benham, sp. nov.; 1 = Makah Formation, LACMIP locs. 8233 and 15911; 2 = Humptulips Formation, LACMIP loc. 12385, 3 = Lincoln Creek Formation, LACMIP loc. 16504.

Table 1

Carbon ($\delta^{13}\text{C}$) and oxygen ($\delta^{18}\text{O}$) stable-isotope analyses of carbonates from the Humptulips Formation (LACMIP loc. 12385) and the Lincoln Creek Formation (LACMIP loc. 16504). All values expressed per mil (‰) relative to PDB standard.

Sample	$\delta^{13}\text{C}$	$\delta^{18}\text{O}$
LACMIP loc. 12385:		
Serpulid? tube wall	- 20.8	- 5.7
Serpulid? tube wall	- 21.0	- 5.7
Serpulid? tube wall	- 26.2	- 5.1
Micrite	- 24.1	- 6.0
LACMIP loc. 16504:		
Micrite	- 44.33	+ 1.6
Micrite ¹	- 46.38	+ 2.6
Fibrous splayed calcite ¹	- 46.73	+ 2.4

¹ Both samples from same hand specimen of carbonate.

Serpulid? tube sample analyses performed by T.M.B. Group, Inc., Miami, Florida; all others by Global Geochemistry Corp., Canoga Park, California.

Stable Isotopes

Isotopic data, $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$, for the Makah Formation carbonate confirmed that it had precipitated from methane-enriched fluids (Goedert & Campbell, 1995). Preliminary isotopic data (Table 1) indicate that the Humptulips Formation and Lincoln Creek Formation carbonates are also methane derived.

Isotopic signatures of serpulid? tube walls and micrite from the Humptulips Formation (LACMIP loc. 12385) are problematic. The $\delta^{13}\text{C}$ values of the tubes (- 20.8 to - 26.2) are similar to some reported for living tube worms from hydrocarbon-seep communities on the Louisiana slope (Brooks et al., 1987). The value for the micrite is close to one sample reported by Goedert & Campbell (1995) from the Makah Formation. These values probably indicate a mixing of methane-derived carbon with less $\delta^{13}\text{C}$ -depleted sources, perhaps dissolved inorganic carbon in seawater and/or particulate and dissolved organic carbon. The unusually low values for $\delta^{18}\text{O}$ may represent diagenetic modification, but they could also indicate elevated temperatures and/or meteoric influence of pore waters, or $\delta^{18}\text{O}$ depletion in marine pore water (Sass et al., 1991).

Samples from the Lincoln Creek Formation (LACMIP

loc. 16504) yielded very negative $\delta^{13}\text{C}$ values (-44.33 to -46.73). As in the Makah Formation carbonate, $\delta^{13}\text{C}$ values this negative are indicative of precipitation from a methane-enriched fluid source (Goedert & Campbell, 1995, and references therein). Values of $\delta^{18}\text{O}$ from the carbonate are positive but they are consistent with precipitation at or near ambient seawater temperatures (K. A. Campbell, personal communication, 1996).

SYSTEMATIC PALEONTOLOGY

Order ARCHAEOGASTROPODA Thiele, 1925

Suborder NEOMPHALINA McLean, 1990

Superfamily NEOMPHALOIDEA McLean, 1981

Family PELTOSPIRIDAE McLean, 1989

Remarks: Warén & Bouchet (1989) considered the family Peltospiridae to be polyphyletic. Living peltospirid genera are differentiated by characters that include soft-part anatomy, radular structure, and protoconch sculpture. Additional studies may justify the reassignment of the genus *Depressigyra* to another family; therefore the current classification is tentative (Warén & Bouchet, 1993). This family has no previously reported fossil record. The genus *Depressigyra* was unintentionally referred to the family Hyalogyrinidae by Lewis & Marshall (1996:189).

Genus *DEPRESSIGYRA* Warén & Bouchet, 1989

Type species: *Depressigyra globulus* Warén & Bouchet, 1989, by original designation. In their diagnosis of the genus *Depressigyra*, Warén & Bouchet (1989:80) stated that the aperture was "distinctly opisthocline," whereas it is actually prosocline. This error was confirmed by A. Warén (personal communication, 1997). Warén & Bouchet (1989) also stated in the diagnosis that the protoconch of *Depressigyra* has a net-sculpture, but in their description of *D. globulus* they stated that the protoconch sculpture was unknown. The original diagnosis of genus *Depressigyra* Warén & Bouchet, 1989, is therefore emended.

Emended diagnosis: Globular peltospirids of medium size; teleoconch almost smooth except for irregular and slightly sinuous growth lines, aperture round and distinctly prosocline; central and lateral teeth of radula unusually slender; no tentacular sexual dimorphism.

Remarks: This genus originally included two species, *D. globulus* Warén & Bouchet, 1989, living only at hydrothermal vents at various sites on the Juan de Fuca Ridge, and *D. planispira* Warén & Bouchet, 1989, living at vent sites on the East Pacific Rise. With additional data on shell and soft-part anatomy from new specimens, *Depressigyra planispira* subsequently became the type species of a new genus, *Planorbidella* Warén & Bouchet, 1993, making the genus *Depressigyra* monotypic.

At least four more gastropod genera living at methane-seeps and having shells similar to *D. globulus*, but possessing distinctive radulae and protoconchs, await description (A. Warén, personal communication, 1997). The protoconchs of all available specimens of both *D. globulus* and the new fossil species are too corroded to preserve any sculpture that may have been present. Therefore, the new species is tentatively referred to the genus *Depressigyra* entirely on the basis of similarity of the teleoconch with that of *D. globulus*. Future studies may warrant reassignment of the new species to another genus.

Depressigyra? statura Goedert & Benham, sp. nov.

(Figure 2A–G)

"Naticid" Goedert & Squires, 1990, p. 1182, fig. 2g; Goedert & Kaler, 1996, p. 67, table 1. "Hyalogyrinid" Goedert & Campbell, 1995, p. 25, figs. 11, 12.

Diagnosis: A *Depressigyra?* with a spire elevated well above the body whorl.

Description: Shell small, globose, thin, nearly smooth except for numerous fine, sinuous, prosocline growth lines; aperture nearly round, prosocline, outer lip thin; whorls convex, suture impressed, spire elevated above body whorl and apex formed by a knoblike protoconch, protoconch surface corroded in all available specimens, appears to be about one whorl; largest shell with 2.25 post-larval whorls.

Comparisons: Except for the slightly more inflated whorls and higher spire, the shell of *D.? statura* sp. nov., resembles that of *D. globulus* Warén & Bouchet (1989: 80–81, figs. 30, 31, 45–47, 51–52, 78, 83). The sculpture of the protoconch of *D. globulus* is not known, the apex of all known specimens having been corroded (Warén & Bouchet, 1989). The only measurement for *D. globulus* is a maximum diameter of 5.4 mm (Warén & Bouchet, 1989:80), and all specimens of *D.? statura* sp. nov., are smaller (Table 2).

Depressigyra? statura sp. nov., somewhat resembles another living chemosynthetic community gastropod in the family Cyathermidae, *Cyathermia naticoides* Warén & Bouchet (1989: 70–72, figs. 6–10, 15, 16, 18, 21–23, 71, 80), but *D.? statura* sp. nov., lacks the very distinct and highly diagnostic deep, rounded notch in the lower part of the aperture.

Material: Holotype, LACMIP 7892, paratypes LACMIP 7893, 7894, 7895, 7896, 7988, LACMIP loc. 16504, Lincoln Creek Formation, late Oligocene. Paratype LACMIP 7897, hypotype LACMIP 8343, LACMIP loc. 12385, Humptulips Formation, middle Eocene. Hypotypes LACMIP 12318, 12319, LACMIP loc. 8233, Makah Formation, early Oligocene. Additional specimens are stored at

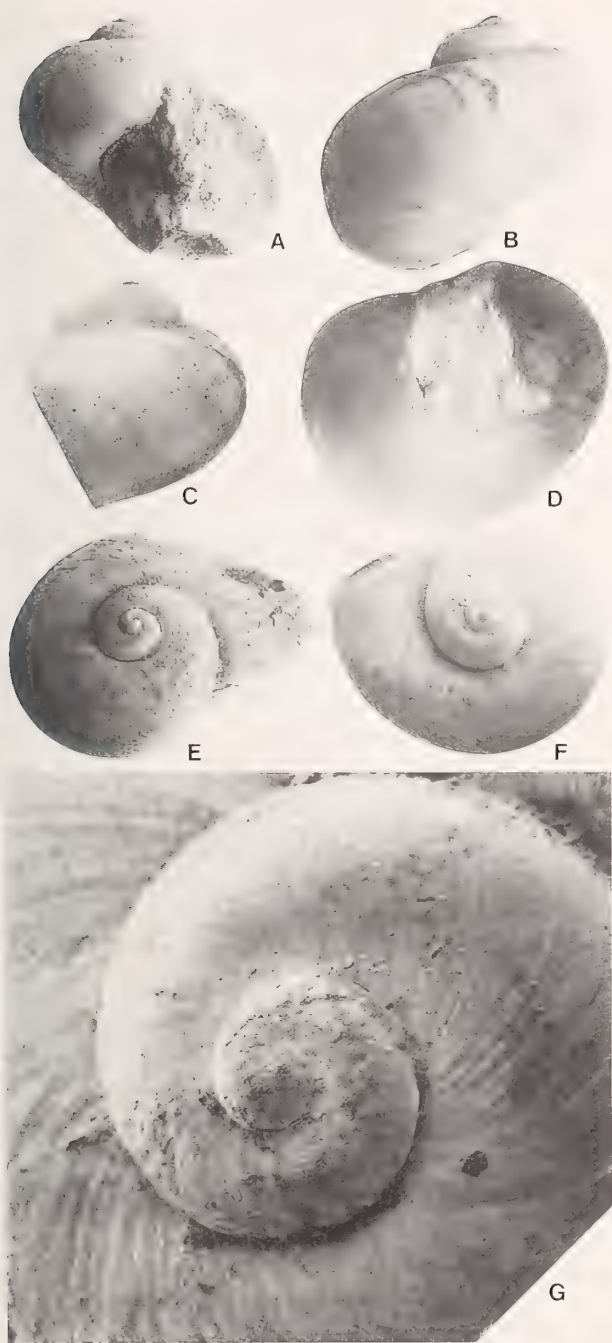


Figure 2

Depressigyra? statura Goedert & Benham, sp. nov., secondary electron micrographs. All from the Lincoln Creek Formation, LACMIP loc. 16504 unless otherwise noted. Outer lip of aperture broken or partially concealed by matrix in all specimens. A. holotype LACMIP 7892, apertural view, X14; B. paratype LACMIP 7893, back view, X14; C. paratype LACMIP 7988, lateral view showing prosocline aperture, X12; D. paratype LACMIP 7895, bottom view, X14; E. paratype LACMIP 7897, Humptulips Formation, LACMIP loc. 12385, oblique top view, X14; F. paratype LACMIP 7894, top view, X14; G. paratype LACMIP 7896, apex showing growth lines, suture, and corroded protoconch, X90.

Table 2

Measurements (in mm) of type specimens of *Depressigyra? statura* sp. nov.; D = diameter, H = height.

Specimen	D	H
LACMIP 7892	2.6	2.9
LACMIP 7893	2.7	2.9
LACMIP 7894	2.8	3.1
LACMIP 7895	3.1	3.4
LACMIP 7896	2.0	2.5
LACMIP 7897	2.4	3.0
LACMIP 7988	2.5	2.6

LACMIP and California State University, Department of Geological Sciences, Northridge (CSUN).

Etymology: The species name, *statura*, Latin meaning stature, is in reference to the high spire, being contrary with the etymology for genus *Depressigyra*, alluding to a low spire.

ACKNOWLEDGMENTS

Gail H. Goedert and Keith L. Kaler assisted with field-work. Isotope analyses were funded and SEM facilities were provided by Pacific Lutheran University (Tacoma, Washington), and Simpson Timber Company (Shelton, Washington) allowed access to one of the localities. We thank Richard L. Squires (CSUN) and Kathleen A. Campbell (NASA/Ames Research Center) for discussions on cold-seep faunas and carbonates. Various drafts of this paper were substantially improved by an anonymous reviewer, Anders Warén (Swedish Museum of Natural History, Stockholm), Philippe Bouchet (Muséum National d'Histoire Naturelle, Paris), James H. McLean and Lindsey T. Groves (LACMIP), Barry Roth, and especially Richard L. Squires (CSUN).

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APPENDIX: LOCALITIES CITED

- LACMIP loc. 8233. Float eroded from bedrock exposed on modern beach terrace at Shipwreck Point, SE1/4 NE1/4 section 36, T. 33 N, R. 14 W, Sekiu River USGS 7.5-minute quadrangle, Provisional Edition 1984, Clallam County, Washington. Upper part of Makah Formation. Age: Early Oligocene.
- LACMIP loc. 12385. Small hill in abandoned meander of the East fork of the Humptulips River, northwest part of Sec. 4, T. 20 N, R. 9 W, Burnt Hill USGS 7.5 minute quadrangle, Provisional Edition 1990, Grays Harbor County, Washington. Humptulips Formation. Age: Middle Eocene.
- LACMIP loc. 15911. *In situ* isolated limestone block within thin-bedded sandstone and siltstone deposits, about 30 m stratigraphically above top of Jansen Creek Member, block measures 1.5 m (N–S) by 2.5 m (E–W), and is weathered out 0.75 m higher than surrounding siltstone; accessible only at low tide. Block is approximately 175 m southeast of tip of Shipwreck Point, SE1/4 NE1/4 Sec. 36, T. 33 N, R. 14 W, Sekiu River USGS 7.5-minute quadrangle, Provisional Edition 1984, Clallam County, Washington. Upper part of Makah Formation. Age: Early Oligocene.
- LACMIP loc. 16504. Limestone block on north side of sharp bend of the Canyon River, 600 m N and 290 m E of SW corner of Sec. 25, T. 21 N., R. 7 W., Grisdale USGS 7.5 minute quadrangle, Provisional Edition 1990, Grays Harbor County, Washington. Upper part of the Lincoln Creek Formation. Age: earliest late Oligocene. This locality was covered by a large landslide in early 1997.

Calyplogena diagonalis, a New Vesicomysid Bivalve from Subduction Zone Cold Seeps in the Eastern North Pacific

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Abstract. A new vesicomysid bivalve species, *Calyplogena diagonalis*, is described from cold seep communities in the Cascadia subduction zone off the Oregon coast and accretionary wedge sediments along the Pacific coast of Costa Rica. Live bivalves and shells were collected at sulfide seeps near 2021 m depth in Oregon and from 2900 to 3800 m depth in Costa Rica. Shell morphology of *C. diagonalis* differs considerably from sympatric congeneric and confamilial species of the northeastern Pacific. Shells are large (to 24.0 cm) and elongate ($H/L = 0.42$), with one or more ridges on the external shell surface extending diagonally from the umbo to near the posteroventral margin. Enlarged, sulfur-colored ctenidia and micrographs of endosymbiotic bacteria held in ctenidia suggest that this species, like other vesicomysids, is a sulfur-based chemolithoautotroph.

INTRODUCTION

The bivalve family Vesicomysidae, first established by Dall & Simpson (1901) includes more than 50 species found nearly exclusively in sulfide-rich habitats such as cold seeps, hydrothermal vents, and accumulations of organic debris (e.g., whale carcasses) from 450 to greater than 3000 m depth. All species investigated have been shown to rely nutritionally on sulfide-oxidizing endosymbiotic chemoautotrophic bacteria held in ctenidia (Fiala-Médioni et al., 1994).

Fossil representatives of the Vesicomysidae are known from as early as the Eocene from the Pacific Northwest, and span the Paleogene and Neogene from collections at several locations (Boss & Turner, 1980; Kanno et al., 1989; Niitsuma et al., 1989; Goedert & Squires, 1993). Although several genera have been erected, most extant species fall under two genera (*Vesicomya* and *Calyplogena*). *Vesicomya* was established in 1886 within the Veneridae (Dall, 1886), and the genus *Calyplogena*, originally placed in the Carditidae, was described in 1891 (Dall, 1891). Assignment of species among genera has resulted in considerable taxonomic confusion within the family, particularly at the generic level (Kojima et al., 1995; Vrijenhoek et al., 1995; Peek & Vrijenhoek, in press). Molecular studies concerning taxonomic affinities within the Vesicomysidae may soon resolve the alignment of species among genera (R. Vrijenhoek, personal communication).

Increased exploration and sampling of vent and seep habitats (and other sulfidic environments) since their discovery in the late 1970s have greatly expanded our un-

derstanding of the natural history and biology of vesicomysids, including description of many new species. Early trawl and dredge samplers were deployed most commonly over soft sediments, thereby undersampling geologically rugged terrain where seep and vent habitats often occur. In addition, these habitats are highly localized, further reducing the likelihood of collections using surface-deployed devices. Recent increases in access to these sites by manned submersibles and remotely operated vehicles have allowed focused investigations of environments typically inhabited by vesicomysids, as well as detailed studies of their natural history. In this paper we describe a new species of vesicomysid bivalve collected from cold seeps associated with accretionary sediments along subduction zones off Oregon and Costa Rica.

COLLECTION INFORMATION

Specimens analyzed for the erection of *Calyplogena diagonalis* sp. nov. were obtained from newly discovered cold seeps in the Cascadia Trough along the Oregon subduction zone (D. Orange, unpublished data), and along the Costa Rica accretionary wedge. A total of 15 live clams or articulated shells were collected at the Oregon site (44°40.56'N, 125°7.08'W) during ALVIN dives (# 2644, 2659, and 2663) at a depth of 2021 m. The Cascadia fauna was dominated by several species of vesicomysid clams (mainly *C. diagonalis*) and bacterial mats, as well as columbellid snails typical of sulfide-rich habitats (e.g., *Mitrella permodesta*). Vestimentiferan worms (*Lamellibrachia* sp.) were also common, but less abun-

Table 1
Paratypes of *Calyptogena diagonalis*

Length (mm)	Height	Width	Site	Valves	Dive #	USNM #
74.2	35.0	30.4	Oregon	Left, Right	2644	(880308)
210.0	86.6	55.1	Oregon	Right	2644	(880309)
226.0	91.0	63.0	Oregon	Right	2644	(880310)
231.0	93.0	58.0	Oregon	Left	2663	(880311)
201.0	77.9	52.1	Coasta Rica	Left, Right	2719	(880312)

dant than vesicomys. Seepage of fluids presumed to be rich in sulfide, methane, or both, appears to be related to dewatering of accretionary sediments during tectonic compression along the Cascadia subduction zone (D. Orange, unpublished).

Twenty-six individuals of *Calyptogena diagonalis* were obtained from seep locations from 2900 to 3800 m depth off Costa Rica, during ALVIN dives # 2715, 2719, and 2728. The Costa Rican site (9°42.28'N, 86°4.38'W) is geographically distant but geologically similar to the Oregon locale, as both are positioned in accretionary complexes undergoing sediment compression owing to tectonic subduction, leading to dewatering of sediments and fluid expulsion at the sea floor (Kahn et al., 1996). The chemosynthetic communities in Costa Rican waters include several species of vesicomysid clams, as well as dense aggregations of serpulid polychaete worms and lamelibrachid vestimentiferans.

Specimens from both sites were compared to vesicomysids housed at the U.S. National Museum of Natural History, the Museum of Comparative Zoology at Harvard University, Los Angeles County Museum of Natural History, and the Santa Barbara Museum of Natural History, and all available published descriptions of vesicomysids. Specimens of *Calyptogena diagonalis* were also sent to other vesicomysid taxonomists for inspection. Owing to the dissimilarity of these specimens from any described extant or fossil vesicomysid species, we concluded that the erection of a new species within the genus *Calyptogena* is justified. Assignment of the new species to the genus *Calyptogena* was based both on its morphological similarity to congeners as well as recent unpublished data from molecular studies confirming the close relationship of *C. diagonalis* to several congeneric species inhabiting the north Pacific (Vrijenhoek, personal communication).

SPECIES DESCRIPTION

Calyptogena diagonalis Barry & Kochevar, sp. nov.

(Figures 1, 2)

Holotype: Length—215.0 mm, height—78.0 mm, width—53.1 mm, sex unknown, collected from Costa Ri-

can cold seep, ALVIN Dive # 2719, 14 February 1994; USNM # 880307, Smithsonian Institution U.S. National Museum of Natural History, Division of Mollusks.

Paratypes: See Table 1.

Type locality: Cold seeps along the Costa Rica subduction zone (9°42.28'N, 86°4.38'W) from 2980 to 3800 m depth. *C. diagonalis* occurs in clusters of 10 to hundreds of individuals partially buried in sediment, in association with other vesicomysid clams and bacterial mats.

Description: Shell whitish, chalky, and covered by dehiscent yellowish brown periostracum. Shell large (to 240 mm long, 95 mm high, and 63 mm wide), elongate, inequilateral, heavy, solid (Figure 1). Valves strongly inequilateral, with slightly inflated, incurved umbo positioned far anterior (18–20% of length). Anterior margin short, rounded, slightly gaping due mainly to outward flexure of left valve. Anterodorsal margin short, slightly convex. Umbonal cavity moderate; beaks mildly inflated. Posterior margin subangular, pointed near ventral end, especially in Costa Rican specimens. Lunule short, sublan- ceolate, poorly defined anteriorly. Posterodorsal margin elongate, convex, angular near distal end. Escutcheon incised steeply immediately posterior to umbo in some specimens. Margin of incision near umbo forming posteriorly directed ridge extending toward postero ventral margin. Ligament deeply embedded, highly inflated, dark brown, lanceolate, calcified along hinge plate in large individuals, encompassing ~16–25% (calcified portion) or ~38–41% (calcified and uncalcified portion) of postero- dorsal margin. Ventral shell margin nearly straight along midpoint in small individuals, mildly concave in large specimens. Sculpture consisting of strong radial ridge from umbo to posteroventral tip, with similar adjacent ribs on some specimens, poorly defined commarginal lir- ations on shell and periostracum, most crowded near an- terior end. Commarginal ridging suggestive of growth rings weakly evident on some specimens. Viewed ven- trally, slight flexure evident along ventral margin, most notably near posterior end. Large individuals with flaky, mostly dehiscent periostracum, except along shell margin, where periostracum overlaps shell margin to provide

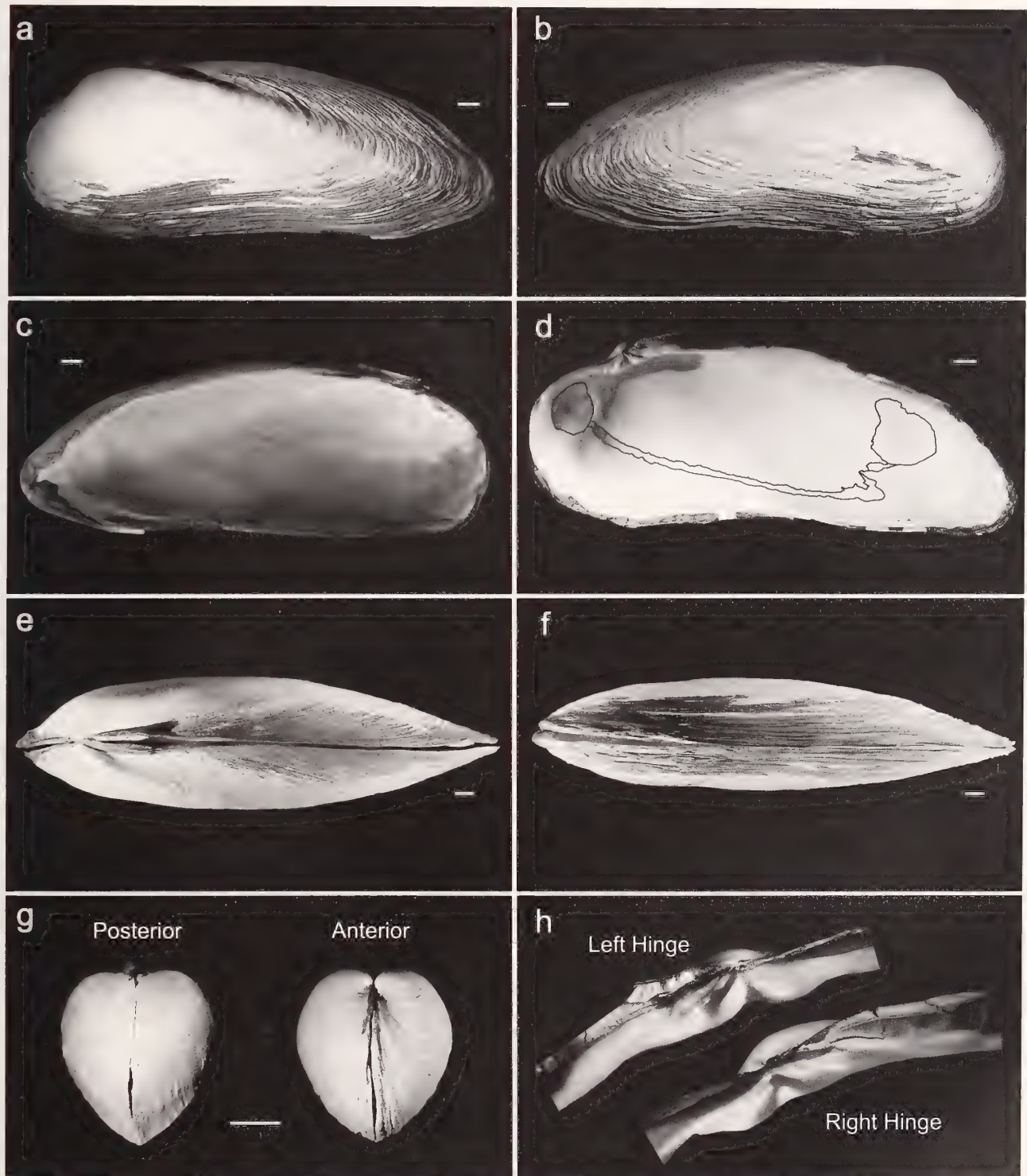


Figure 1

Diagnostic shell characteristics of *Calyptogena diagonalis* Barry & Kochevar, sp. nov. Scale bars = 1 cm. a. External view of left shell valve of holotype (USNM# 880307) from Costa Rican collection. b. External view of right shell valve of holotype. c. Internal view of left shell valve of holotype. d. Internal shell valve of paratype (USNM# 880312) from Costa Rican site, with pallial line and adductor muscle scars highlighted in black. e. Dorsal view of holotype. f. Ventral view of holotype. g. Anterior and posterior views of juvenile specimen (paratype; USNM# 880308) from Oregon seeps. h. Hinge structure of left (paratype; USNM# 880311) and right (holotype) valves.

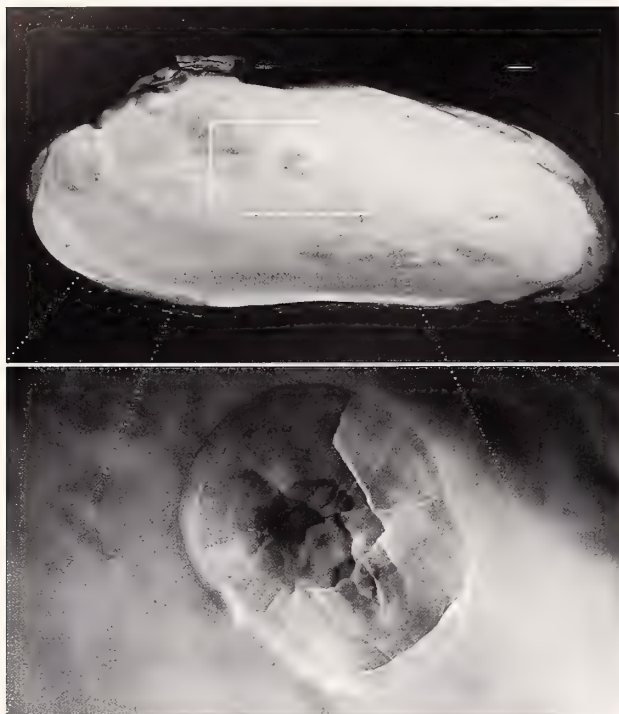


Figure 2

Repaired internal surface of shell valve from Oregon specimen (paratype; USNM# 880310). Scale bar = 1 cm. a. Overall view of internal valve, with repaired shell area highlighted. b. Magnified view of shell repair.

complete seal when shell valves closed. Periostracum inflated, ruffled along anterior to anteroventral margin. Dissolution of external shell moderate to extreme in some specimens, principally ventral and posterior to umbones. Fenestrations resulting from dissolution occasionally repaired by localized calcification of inner shell (Figure 2) in some specimens.

Right valve with two cardinal teeth beneath umbo (Figure 1d, h). Anterior cardinal tooth strongly protuberant, with parallel to subtrigonal borders, pointing ventrally from umbo, and convex to slightly concave medial surface. Posterior tooth dorsal to anterior cardinal, protuberant, narrow, and slightly bifid in some. Anterior and posterior cardinals joined under beak. Three sockets formed by cardinal teeth and umbonal shell margin to accept cardinal teeth from left valve, central socket deepest, triangular. Posterior hinge plate massive, forming nymph subtending and partially enveloping ligament; longest relative to shell length in small specimens.

Left valve with three cardinal teeth and two sockets to accept central and dorsal cardinal teeth of right valve (Figure 1c, h). Anterior cardinal strongly protuberant, narrow to massive, rounded medially; convex anterior margin merges ventrally with hinge plate, flat posterior face contacts anterior cardinal of right valve. Central car-

dinal tooth massive, strongly protuberant, trigonal, pointed to nearly blunt; anterior surface convex, posterior contact surface flat. Posterior cardinal positioned dorsally, small compared to other teeth, long, narrow, produced only slightly above hinge plate, nearly horizontal; medial surface nearly smooth to mildly serrate.

Internal shell surface porcellaneous with faintly developed radial internal riblets and minor commarginal undulations. Anterior adductor muscle scar recessed dorsally and posteriorly, ovately conic to subelliptical, with minor concentric lirations, extending to anterior shell margin in small individuals (Figure 1d). Posterior adductor muscle scar larger, irregularly ovate, teardrop-shaped, or pear-shaped, pointed dorsally, lacking supportive shell sculpture found in anterior scar. Pallial line weakly evident, broad, with sinuous and irregular margins, mildly convex anteriorly and ventrally, and angular posteriorly, forming small pallial sinus (Figure 1d).

Soft anatomy: Our general description of the soft anatomy of *Calyplogena diagonalis* is based on dissections of two adult-sized individuals. Soft anatomy is generally similar to that reported for *C. pacifica* Dall, 1891; *C. kilmeri* Bernard, 1974; *C. magnifica* Boss & Turner, 1980; *Ectenagena extenta* Krylova & Moskalev, 1996; and *C. packardana* Barry et al., 1997. The most conspicuous features of all six species are the greatly enlarged and often sulfur-colored ctenidia, large and heavily vascularized foot, reduced digestive system, and red, hemoglobin-rich blood, which all relate to their chemosynthetic life style.

Mantle and siphons. Mantle lobes bilaterally symmetrical, thickened around shell margin, particularly near anteroventral margin, attached to shell by thick, broad pallial muscles. Mantle cavity opens to create pedal gape from ventral margin of anterior adductor muscle to ventral anterior margin of incurrent siphon. Thick folds of inner mantle fused posteriorly to form separate incurrent and excurrent siphons; fusion extends dorsally between adductor muscles. Mantle margin thickened and inflated along anterior margin. Band of sensory papillae along thickened anterior mantle margin, similar to that described for *C. magnifica* (Boss & Turner 1980).

Incurrent and excurrent siphons formed by fusion of the mantle, conical to cylindrical in side view, ovate in cross section, positioned in pallial sinus formed by folds of thickened mantle musculature. Highly developed pallial musculature near posteroventral shell margin in siphonal region, as in *C. magnifica* (Boss & Turner, 1980). Incurrent siphon larger and more ovate than excurrent siphon. Distal margin of both siphons uneven, slightly serrate, lacking papillae found in *Calyplogena packardana* (Barry et al., 1997). Densely branched structure near base of incurrent siphon functions as filter to reject large particles. Excurrent siphon smaller in cross section than incurrent siphon, with mildly serrate distal margin, thin collar of tissue lining internal siphonal walls to form

one-way valve similar to other vesicomys (Bernard, 1974; Barry et al., 1997).

Ctenidia: Greatly enlarged ctenidia enveloping body along length, from umbonal cavity ventrally through much of shell cavity. Inner and outer demibranchs on each side of body with ascending and descending lamellae. Inner demibranchs fused along distal margins to middle of visceral mass and joined posteriorly, isolating incurrent and excurrent pallial chambers. Ctenidia variously colored among specimens, from bright sulfur yellow to purplish red, presumably depending upon content of elemental sulfur in endosymbiont bacteriocytes (Kochevar & Barry, 1994). We have observed ctenidia of *C. packardiana*, *C. pacifica*, and *C. kilmeri* to change gradually from sulfur-colored to deep red in laboratory aquaria, apparently due to endobacterial oxidation of elemental sulfur deposits. Micrographs of ctenidial tissues show endosymbiotic bacteria similar to those in related chemosynthetic vesicomys (R. Kochevar, unpublished data).

Foot and visceral mass: Foot large, generally conical, highly muscular and distensible, particularly in its ventral half; highly vascularized, deep red owing to hemoglobin content. Dorsally, foot grading into visceral mass, housing large gonad surrounded laterally and ventrally by foot musculature, and dorsally by stomach, digestive gland, intestinal tract, and heart. Labial palps, stomach, and intestine greatly reduced, similar to other vesicomys (Bernard, 1974; Boss & Turner, 1980; Barry et al., 1997).

Reproductive system: Microscopic inspection of gonad samples from several specimens indicates that *Calyptogena diagonalis* is gonochoristic. Ovary or testis found directly dorsal to foot and surrounded by foot musculature. No evidence of sexual dimorphism in shells or soft anatomy other than the gonad was observed.

REMARKS

Calyptogena diagonalis inhabits seep communities associated with accretionary complex sediments near 2021 m depth off Oregon and from 2900 to 3800 m off Costa Rica. Owing to its broad latitudinal range, we suspect that this species inhabits other sulfide-rich seeps along continental borderlands of the northeastern Pacific. Observations during ALVIN dives found *C. diagonalis* in clusters including ~10 to 100 individuals, buried partially in sediments presumed to be the locus of seeping sulfide-rich pore fluids. *Calyptogena pacifica* and other vesicomysid clams cohabit seeps with *C. diagonalis*.

The principal diagnostic shell characters of *Calyptogena diagonalis* are its large size, elongate shape, diagonal ridge along the posterior apex of each valve to near the posteroventral shell margin, and somewhat angular posterodorsal margin.

Allometric changes in shell morphology, determined from comparisons of three juvenile shells with five to 10

adult-sized shells, is evident in several shell characteristics of *C. diagonalis*. Juveniles are considerably less elongate (H/L ~0.55 [juveniles] versus ~0.39 [adults]), more inflated (W/L ~0.41 [juveniles] versus ~0.25 [adults]), and less inequilateral (umbo ~24% along length [juveniles] versus ~19% [adults]).

While direct measures of chemosynthetic physiology in *C. diagonalis* are lacking, all available evidence indicates that this species relies on sulfur-oxidizing endosymbiotic bacteria for most or all of its nutrition. All species of vesicomysid bivalves investigated have been shown to derive their nutrition from thiotrophic endosymbionts (Fiala-Médioni et al., 1994). *C. diagonalis* inhabits seep environments and has morphological (size, soft anatomy, endosymbiotic bacteria, elemental sulfur in ctenidial tissues, hemoglobin) and behavioral (inhabits seeps, aggregates at sites presumed to have sulfide-rich pore fluids) characteristics very similar to known chemosynthetic vesicomysids. Analysis of stable carbon isotopic ratios of foot tissues for *C. diagonalis* also suggest chemosynthesis as the primary nutritional pathway, with values near 36‰, similar to confamilial species known to rely on chemosynthetic production.

Geographic Variation in the Morphology of *Calyptogena diagonalis*

Calyptogena diagonalis from sites off Oregon and Costa Rica differs slightly in shell morphology and may warrant the specification of distinct subspecies for the two groups, though additional collections are required to resolve consistent differences among these geographical groups. Shells of Oregon specimens are slightly deeper-bodied than their Costa Rican counterparts, with height/length ratios averaging 0.41 (s.d. = 0.02) and 0.38 (s.d. = 0.03), respectively (shells > 150 mm length; t-test = ns). Southern material also has a less inflated ligament, and more prominent secondary diagonal ridge dorsal to the primary ridge, leading from near the umbo to the angle in the postero-dorsal margin. Dentition is very similar, with minor variation in shape and orientation of cardinal teeth. The anterior cardinal of southern specimens is more protuberant and directed more anteriorly, compared to the nearly vertical orientation of northern specimens.

Comparison with Other Vesicomysids

Calyptogena diagonalis is similar to few extant described vesicomysids, owing principally to its large size. *Ectenagena extenta* inhabits seep communities with *C. diagonalis*, but is considerably more elongate (H/L ~ 0.22), and lacks the characteristic diagonal ridge of *C. diagonalis* (Table 2). Similarly, *Calyptogena phaseoliformis* Métivier et al., 1986, at present known only from the western Pacific, may be confused with *C. diagonalis*, but is also highly elongate (H/L ~ 0.24). Morphometric ratios of *C. diagonalis* are more similar to *Calyptogena mag-*

Table 2
Comparison of morphometric ratios among described extant vesicomysid species
similar in morphology to *Calyptogena diagonalis*

Species	Height/Length (H/L)			Width/Length (W/L)			Width/Height (W/H)		
	Mean	S.D.	N	Mean	S.D.	N	Mean	S.D.	N
<i>Calyptogena diagonalis</i> , sp. nov.	0.42	0.07	38	0.29	0.07	36	0.69	0.07	35
<i>Calyptogena elongata</i>	0.45	0.02	12	0.26	0.08	12	0.58	0.19	12
<i>Calyptogena kilmeri</i>	0.51	0.03	1805	0.33	0.03	1826	0.65	0.06	1825
<i>Calyptogena magnifica</i>	0.44	0.02	14	0.27	0.02	5	0.61	0.05	5
<i>Calyptogena packardana</i>	0.53	0.03	210	0.31	0.03	210	0.58	0.04	210
<i>Calyptogena phaseoliformis</i>	0.24	0.01	6	0.16	0.01	4	0.65	0.04	4
<i>Ectenagena extenta</i>	0.22	0.01	4	0.17	0.01	4	0.78	0.05	4

nifica than any materials examined, but these species differ greatly in shell outline and sculpture, ligament size and shape, and periostracum morphology. Valves of *C. magnifica* are subelliptical with similarly rounded anterior and posterior margins, and lack either the pointed posterior margin or diagonal ridge sculpture characteristic of *C. diagonalis*. The ligament of *C. magnifica* is massive and much more extensive than *C. diagonalis*, extending from the umbo to the posterior pedal retractor muscles (~ 48–50% of posterodorsal margin versus 38–41% in *C. diagonalis*). The periostracum of both species develops complex and inflated folds along the anterior margin, but these appear to be more extensive in *C. magnifica* as reported by Boss & Turner (1980). In addition, *C. diagonalis* and *C. magnifica* inhabit different environments and appear to be endemic to cold seeps and hydrothermal vent sites, respectively. *Calyptogena elongata* Dall, 1916, is similar in shape, but does not reach the large size of *C. diagonalis*, is thinner, and lacks a diagonal ridge. *Calyptogena packardana* is generally similar to small specimens of *C. diagonalis*, but is easily distinguished by its very narrow width to length ratio (0.31) and deeply incised escutcheon. Finally, two morphologically similar species, *Calyptogena kilmeri* and *Calyptogena soyoae* Okutani, 1957, from the northeastern and northwestern Pacific, respectively, could be confused with small *C. diagonalis*. However, like *C. packardana*, both species lack a diagonal ridge, and have very different hinge dentition than *C. diagonalis*. The posterior (dorsal) cardinal tooth of the right valve in these smaller species is directed at nearly 45° toward the posteroventral margin. In *C. diagonalis*, this tooth inclined only about 20 to 30 degrees from parallel with the dorsal shell margin.

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Histological Description of the Gonad, Reproductive Cycle, and Fertilization of *Pisidium amnicum* (Müller, 1774) (Bivalvia: Sphaeriidae)

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Abstract. A detailed study of the reproductive cycle of a Spanish population of *Pisidium amnicum* (Müller, 1774) based on monthly histological gonadal samples is presented. Results of the study of the gonadal cycle perfectly match previously reported data on the dynamics of this population, with mature gametes of both sexes present between July and October. Specimens surviving one reproductive cycle undergo a second gametogenesis resulting in a new brood. Nevertheless, most of them die before birth because of the adults' limited life span. We suggest that cross-fertilization in these freshwater bivalves occurs in summer in the gills or in the suprabranchial chamber instead of in the gonoduct as has been proposed by other authors. Illustrations of all stages of the gametogenic processes, both male and female, as well as of the first stages of embryonic development, are given. Differences between the reproductive strategies of *P. amnicum* and other sphaeriid species are also discussed.

INTRODUCTION

All species of the family Sphaeriidae studied are hermaphroditic and incubatory, retaining fertilized eggs in brood sacs developed in the inner gills. Following Mackie (1978), who reviewed the terms ovoviviparity and viviparity, these freshwater bivalves are ovoviviparous. The main literature about reproduction, with histological studies of species of the family Sphaeriidae, deals with the genera *Musculium* Link, 1807 (Okada, 1935a, b, c, 1936; Heard, 1977) and *Sphaerium* Scopoli, 1777. (Gilmore, 1917; Woods, 1931, 1932; Thomas, 1959; Heard, 1977). The only authors who studied the gonadal histology of species of the genus *Pisidium* Pfeiffer, 1821, were Heard (1965), who focused on the reproductive strategies of the North American species, and Meier-Brook (1970) who dealt with several European species, not including *Pisidium amnicum* (Müller, 1774).

The population dynamics of *P. amnicum*, the largest species of the genus, has been studied in Germany (Danneel & Hinz, 1976), England (Bass, 1979), Canada (Vincent et al., 1981), and Spain (Araujo et al., in press), but no data exists about its gonadal development or its reproductive cycle from a histological point of view. Recently, Araujo & Ramos (1997) described the gonadal morphology and evidence of intrafollicular fertilization in several specimens of this species, discussing the possibility of self-fertilization.

This paper describes histologically gametogenesis, the cellular types of germinal lineage, reproductive cycle, and

fertilization process of a Spanish population of *P. amnicum* previously studied by Araujo et al., (in press). It shows that this isolated population, the southernmost of the species in Europe and in the world (except for the North African population cited by Kuiper in 1972), is very well adapted to local conditions as indicated by its breeding success compared with North European populations of the species (Araujo et al., in press).

MATERIALS AND METHODS

Specimens of *P. amnicum* were collected monthly between June 1990 and May 1991 in the Miño River in the NW of the Iberian Peninsula. A description of the sample site, sampling methods, and water physico-chemical characteristics are provided by Araujo et al., (in press). In the laboratory, each monthly sample was sorted into 1 mm size classes. Four specimens of 6–7 mm were used to determine which of four protocols was best for fixation: (a) immersion of specimens in hot water (6 seconds, 60°C) and fixation with 70% ethanol; (b) direct fixation in formalin saline solution (100 mL 40% formalin, 9 g sodium chloride and 900 mL distilled water); (c) immersion in hot water (6 seconds, 60°C) and fixation with formalin saline solution; and (d) relaxing specimens with menthol (24–72 hrs), and fixation with formalin saline solution. The second method produced the best results and was used in the study. Fixed specimens were removed from their shells, dehydrated in a graded ethanol series (30, 50, 70, 96, and 100%) and embedded in paraffin. Sections were made between 7–10 µm and stained with hematoxylin-eosin and Heidenhain's azan. Those specimens containing shelled larvae in the gills were submerged in a mixture of 70% ethanol and 1% acetic acid

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for 3 days in order to decalcify the embryonic shells, as proposed by Okada (1935a). We were normally successful when we decreased this time to 24 hr.

As the months in which embryos and/or larvae grow inside the maternal gill, and the month of juvenile release were already known (Araujo et al., in press), the fertilization and first stages of cleavage were mainly studied in specimens from August and September. Thus, we studied 13, 14, six, four, and two specimens from September, August, June, July, and October, respectively, and one from the rest. In order to analyze the gametogenetic stages, adult specimens of 7–8 mm were observed. Once we knew the months of greater gametogenic activity and the size at which the species reaches sexual maturity, specimens of all size classes from these months were observed.

RESULTS

P. amnicum is a simultaneous hermaphrodite, as both male and female gametes develop in the gonad of each sexually mature specimen at the same time. Male and female tissues are organized in follicles, the male fraction being much larger than the female and occupying the anterior part, while the small ovarian fraction is posterior (Figure 1A, B). Although there are no hermaphroditic follicles, both gonadal fractions overlap near the hermaphroditic ducts, which are exterior and lateral, running parallel to the cerebro-visceral connectives (Figure 1C). As has been demonstrated by Araujo & Ramos (1997), male and female gametes are commonly found together in this area.

Gametogenesis

The simultaneous presence of mature spermatozoa and ripe oocytes was restricted to the period from July to October. Specimens born in April–May undergo gametogenesis in summer. The larger gravid specimens found from June to September were the survivors of the previous year in which the gametogenetic activity restarts, although most of them die before the new cycle finishes. Fertilization and settlement of the zygotes occur in late summer (August and September) in both newborn spec-

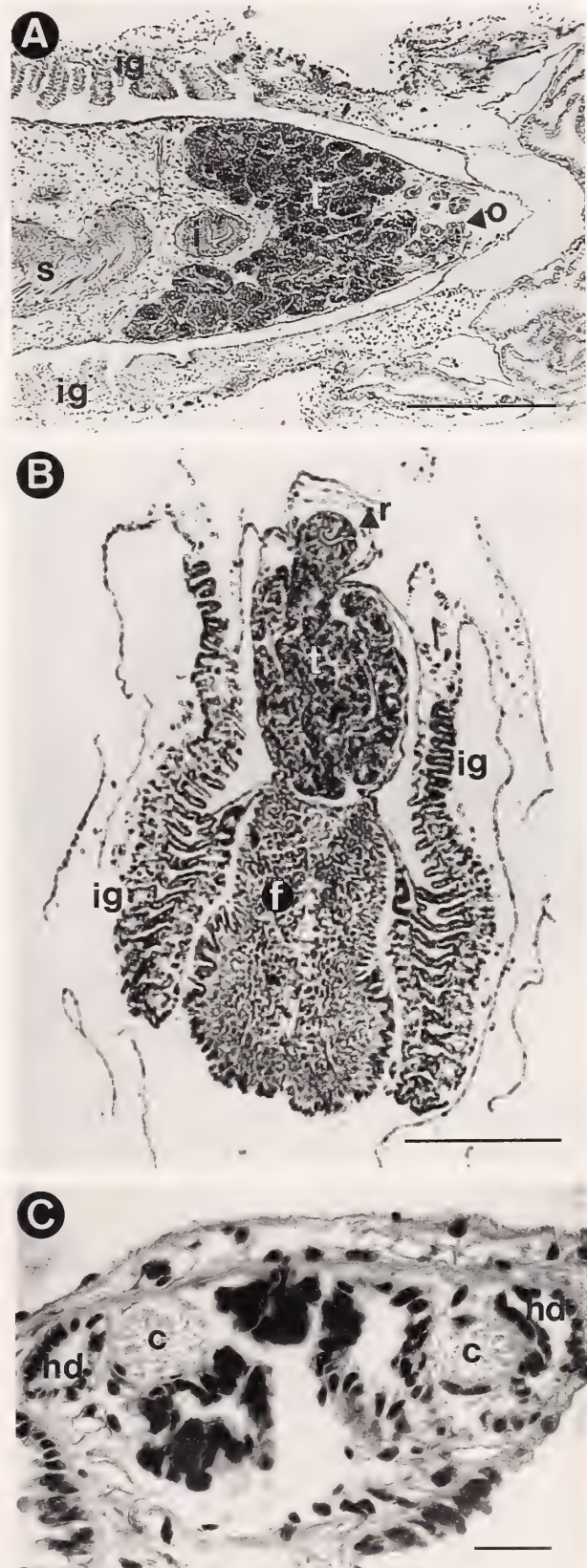


Figure 1

Gonad of *P. amnicum*. **A.** Longitudinal section of an 8–9 mm specimen from August. The anterior part is at left. Scale bar = 1 mm. **B.** Transverse section through the gonad of a 4–5 mm specimen from August. Scale bar = 0.5 mm. **C.** Transverse section through the end of the gonad showing the hermaphroditic ducts and the connectives. Scale bar = 50 μ m. c, connectives; f, foot; hd, hermaphroditic ducts; i, intestine; ig, inner gill; o, ovary; r, rectum; s, stomach; t, testis.

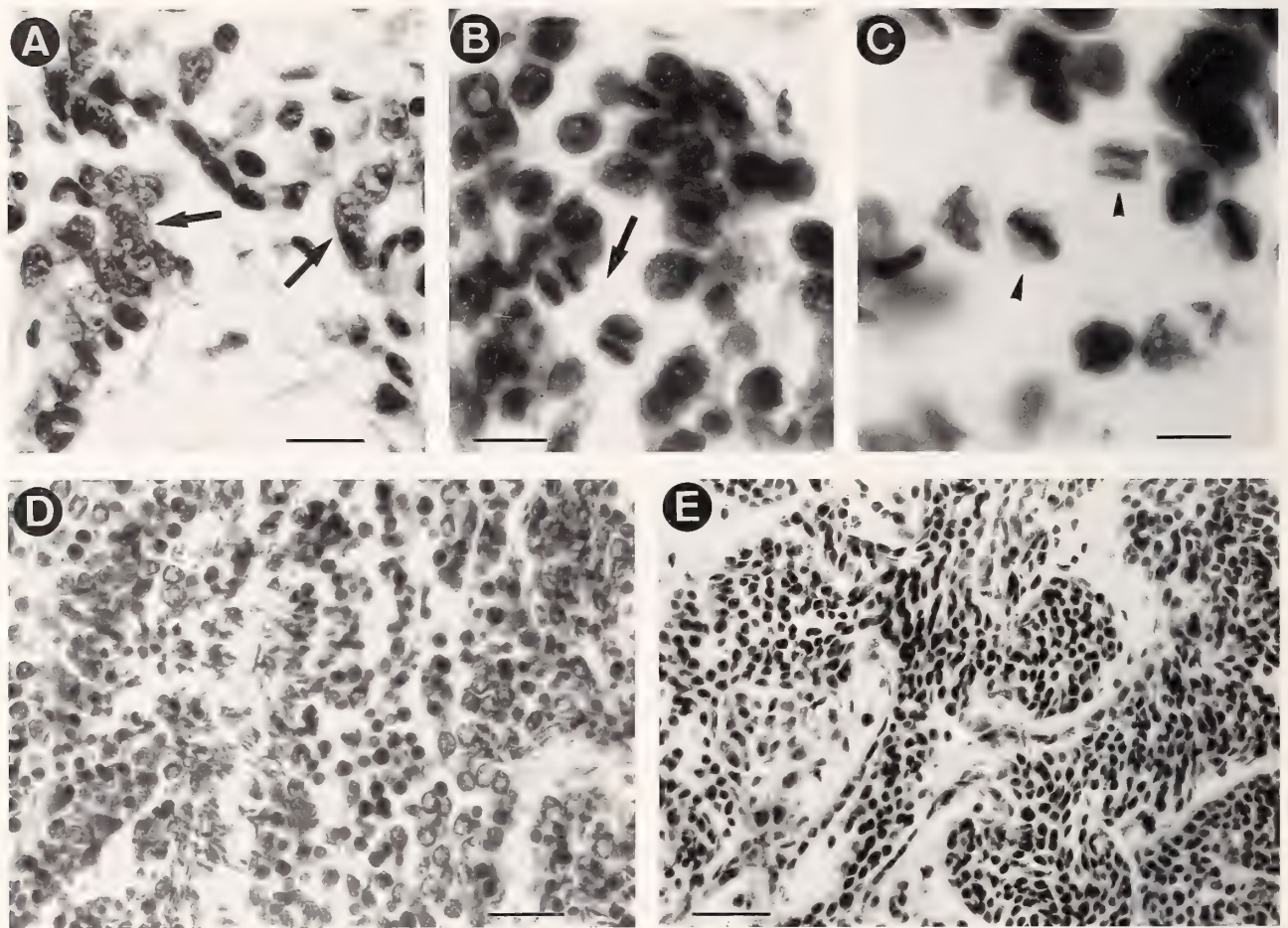


Figure 2

Spermatogenesis of *P. amnicum*. **A.** Spermatogonia (arrows). Scale bar = 30 μm . **B.** Spermatocytes I. The arrow shows the anaphase of first division. Scale bar = 20 μm . **C.** Spermatocytes II. The arrow heads show the metaphase and anaphase of second division. Scale bar = 12 μm . **D.** Section of testis showing different stages of spermatogenesis. Scale bar = 40 μm . **E.** Testis of a specimen from January. Scale bar = 75 μm .

imens and ones from the previous generation. Gravid animals collected during these months still presented many mature oocytes and spermatozoa.

Maturation of the male gametes occurs in specimens from May to October, the light in the middle of the follicles increasing at the same time as spermiogenesis occurs. In October, the follicles are empty, with many spermatogonia growing from their walls; this evacuation phase is followed by a proliferation phase from November to April, with full and compact follicles without light inside.

Spermatogonia were present in the testis from April to December. They are large cells (cell diameter = 10–12 μm) with very little cytoplasm, adhering to the follicle walls (Figure 2A). The nucleus is full of chromatin granules so it is difficult to ascertain the number of nucleoli. First order spermatocytes (Figure 2B) are cells with a

diameter of 7–8 μm , scant cytoplasm, and the chromatin spreading in a large nucleus. When these cells are found in the middle of the follicle, the chromatin appears at the edge of the nucleus. Second order spermatocytes are smaller (4–6 μm), and we have also found them in metaphase and anaphase II (Figure 2C) prior to development of the spermatids (2–3 μm). The condensation of the genetic material at this last stage makes it easier to see the cytoplasm than at previous stages. The head of the mature spermatozoa is about 5–6 μm , and the tail is very difficult to see. In July all the male cellular lineage is easily observed in the same follicle (Figure 2D).

In specimens between 4 and 6 mm from August and September (those born in May of the same year), the spermiogenesis is in the latter stages. From July to September, spermatogenesis has restarted in the largest (> 7 mm) and old specimens. In October the testis is massive,

full of polyhedral cells (Figure 2E), with conjunctive tissue in the interfollicular space. The testis remains at this stage for the rest of the winter until late spring and summer when spermatogenesis restarts. The process in the female tissues is very similar. Previtellogenic oocytes are present in August and September in specimens born in May of the same year. After spawning, the ovogenesis restarts in the oldest specimens. The oogonias adhere to the follicle walls. They are cells similar to the spermatogonias with a diameter of about 20 μm . They have a large nucleus that occupies most of the cell, having a refringent light nucleolus and scattered particles of chromatin, very visible both in azan and hematoxylin-eosin stained slides. A second nucleolus and accompanying cells attached to the oogonias can be observed (Figure 3A). The previtellogenic oocytes are still attached to the follicle wall; they are about 20 μm in diameter with a 15 μm nucleus, showing one or two nucleoli (Figure 3B). Previtellogenic oocytes still maintain accompanying cells (Figure 3C) and sometimes have an anphinucleolus in the nucleus. At the end of the previtellogenic stage, the heterogeneity of the nucleus increases and the accompanying cells disappear. At this state, spherical corpuscles resembling the nuclei of the oocytes can be seen in the female follicles of specimens up to 6–7 mm (Figure 3D). At the beginning of the vitellogenesis, the oocyte size increases and the nucleus still contains the nucleoli and the anphinucleolus (Figure 3E). The ripe oocytes, now free from the acinar wall, are about 40–60 μm and have a nucleus of 12 μm with one or more nucleoli, the larger ones sometimes having an anphinucleolus (Figure 3F).

In specimens from September, the above mentioned spherical corpuscles only appear in specimens over 4 mm.

No signs of reabsorption were observed within the ovarian tissues after ova release, but differentiation of the oogonia immediately follows this event.

During August and September, the largest amount of mature male and ripe female gametes appears, often occurring together within female follicles near the hermaphroditic duct, allowing the occurrence of self-fertilization.

P. amnicum becomes sexually mature at a shell length of about 3–5 mm, the male gonad probably maturing first (we detected one mature specimen of 3–4 mm) and the female later (4–5 mm). Testis maturation proceeds from the anterior to the posterior area, and from the center to the periphery.

Fertilization and Brooding

Only once did we observe a mature oocyte in the hermaphroditic duct, and it had not been fertilized.

No gravid specimens appeared among those from June and July that were studied histologically. In the specimens from August, three histological observations indicated recently fertilized oocytes (zygotes) in the inner

gills. In one case, the zygote had a nuclear membrane with many nucleoli and the male pronucleus (Figure 4A). In the other two, the zygote had lost the nuclear membrane, the male pronucleus was located at the edge of the cell, and the female pronucleus was in meiotic metaphase (Figure 4B, C, D). Embryos at several stages of cleavage were also found. Figure 4E, F shows respectively, one embryo in a stage prior to blastula and one blastula, and Figure 4G shows the arrangement of the embryos within the parental gill.

During August and September when the first stages of the embryos were observed, several gravid specimens carried embryos in even more advanced stages, i.e., the ova had been fertilized and had begun the cleavage process once they fell between the gill filaments.

The germ cells from which the gonads develop were observed during all the cleavage of the embryo from the blastula (Figure 5A) to the prodissococonch larvae (Figure 5B) (the one shelled and still covered by the brood sac within the marsupium).

DISCUSSION

The simultaneous occurrence of mature male and female gametes in *P. amnicum* specimens over 5 mm collected from July to October, particularly in August and September, means that this species, like the other of the family Sphaeriidae studied by Meier-Brook (1970), is a simultaneous hermaphrodite (see Araujo & Ramos, 1997). This agrees with Meier-Brook's (1970) point that the simultaneous occurrence of mature gametes of both sexes in 3 mm specimens of *Musculium heterodon* (Pilsbry) suggests that the species is, for most of its life, a simultaneous hermaphrodite, although the male fraction probably matures before the female one. This agrees with Okada's (1935b) concept of protandric maturation. However, following Hoagland (1984), the term protandric should describe animals that can change their sex from male to female without reverting to male. Therefore, this term does not apply to the Sphaeriidae.

Regarding the reproductive habits of this species, histological analysis of the gonads of *P. amnicum* confirms the reproductive strategy (semelparous and univoltine) postulated by Araujo et al. (in press) on the basis of population dynamics. This strategy differs from the rest of the European species of the genus, which, according to Meier-Brook (1970), are iteroparous and multivoltine.

After spawning (gamete release), there is a growth period of the germinal cells in the gonads, which is very long and slow in *P. amnicum*, especially in the female. In *P. lilljeborgii* Clessin, 1886, this growth is quicker, allowing two reproductive periods in the same year. The lack of mature female gametes immediately after spawning (as occurs in *P. lilljeborgii*) and the long gravidity period in *P. amnicum* (nearly 9 months) compared with

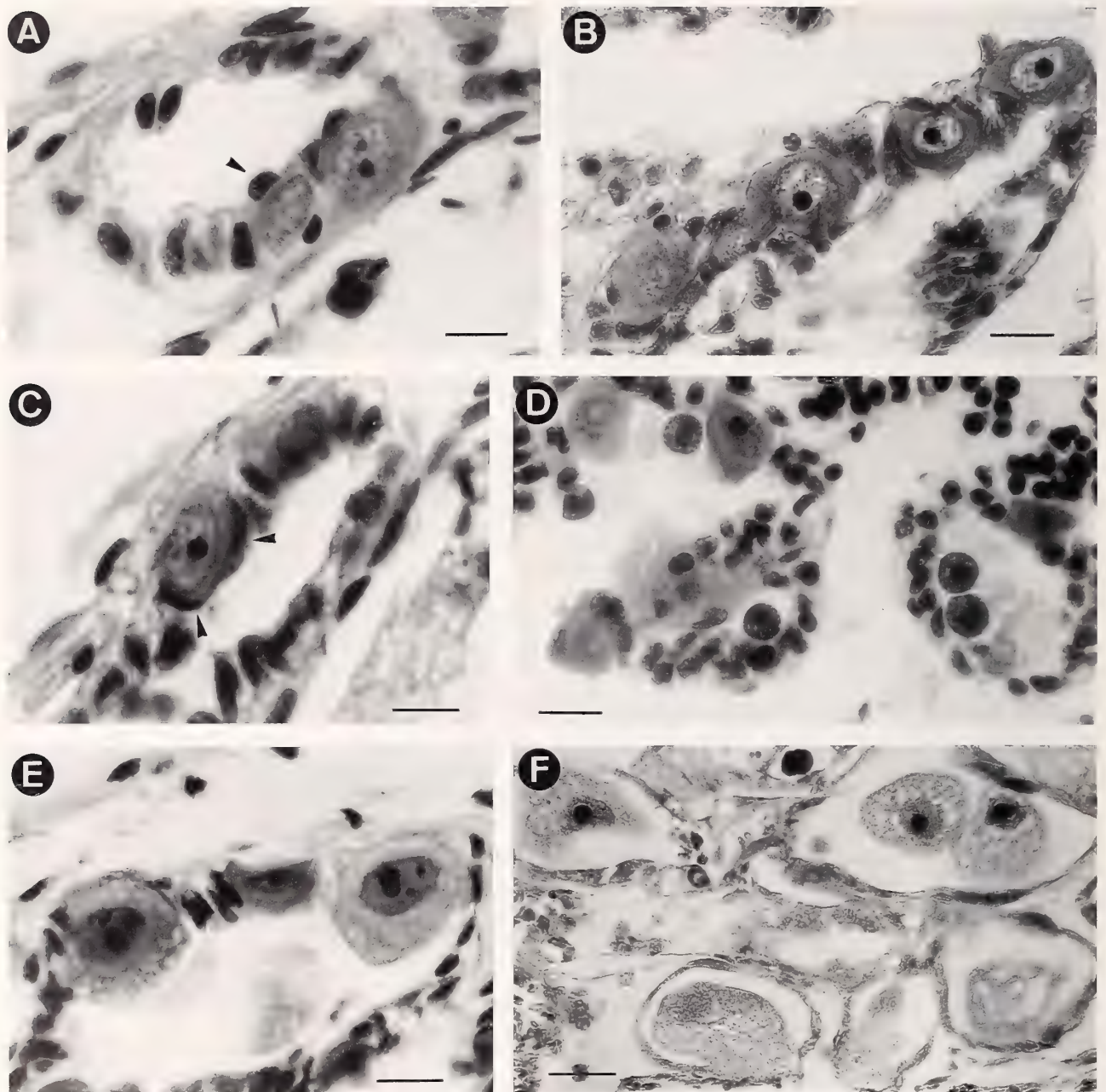


Figure 3

Oogenesis of *P. amnicum*. **A.** Oogonia with accompanying cells (arrow head). Scale bar = 20 μm . **B.** Oocytes. Scale bar = 30 μm . **C.** Oocyte with accompanying cells (arrow heads). Scale bar = 20 μm . **D.** Refringent corpuscles in the ovary (specimen from June). Scale bar = 30 μm . **E.** Oocytes with several nucleoli and anphinucleolus. Scale bar = 30 μm . **F.** Ripe ova in the ovary of a specimen from August. Scale bar = 40 μm .

other species (2 months in *P. lilljeborgii*) also help to explain this difference.

Our results confirm the absence of an extended life span or a successful second brood in *P. amnicum* from southern areas. Although the gametogenetic processes are

reactivated once the single reproductive cycle occurs, this cycle is not completed because the species' limited life span (15 months, Araujo et al., in press) means specimens die before the brood is fully developed. In other words, those that die in summer are always gravid. This phe-

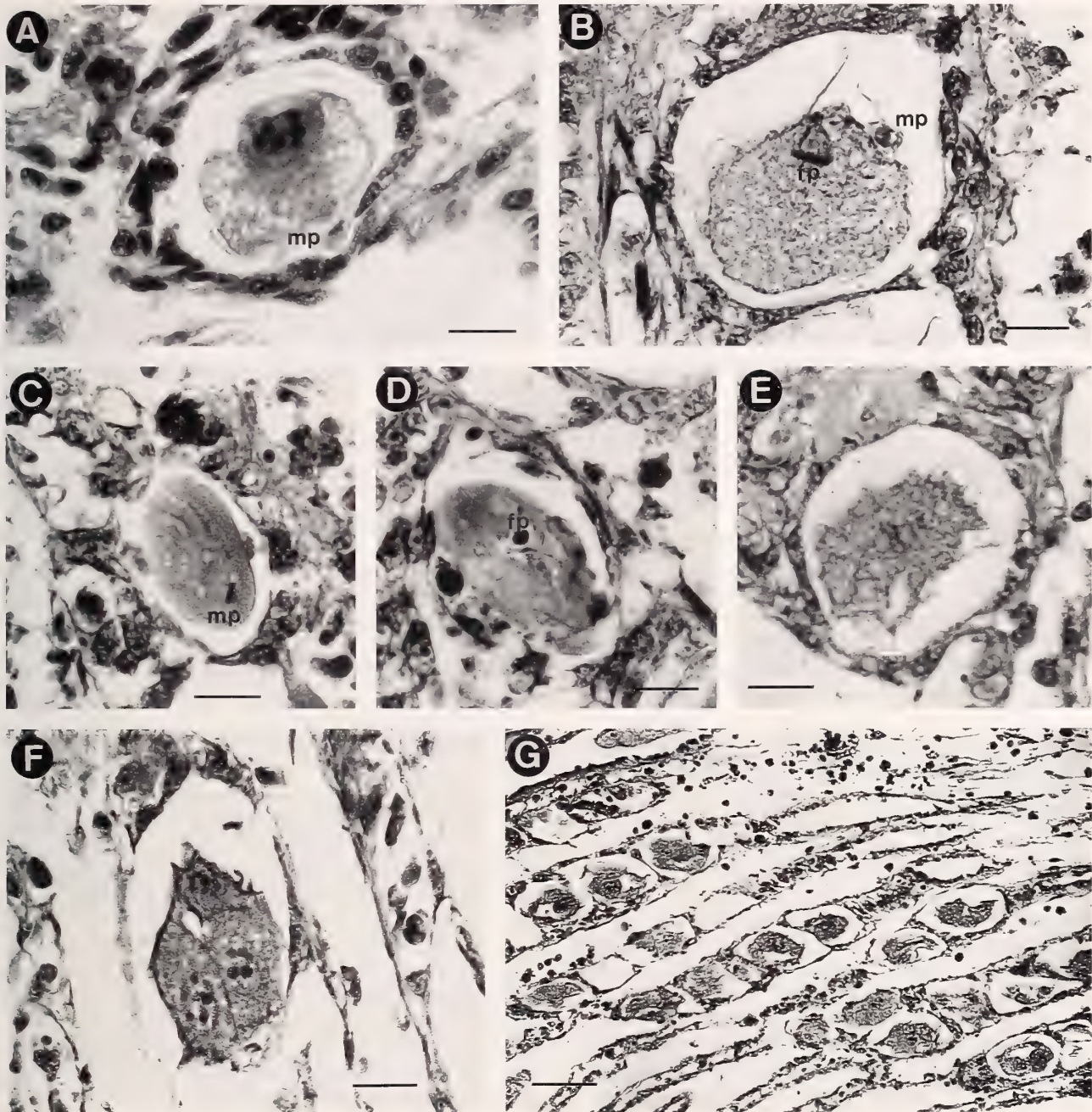


Figure 4

Fertilization of *P. amnicum*. **A.** Zygote in the gill filaments. **B.** Meiosis of a zygote in the gill filaments. **C, D.** Consecutive sections of a zygote in the gill filaments. **E.** Mitosis of an embryo. **F.** Blastula. From A to F, scale bars = 30 μm . **G.** Arrangement of the recently formed zygotes in the gill. Scale bar = 120 μm . mp, male pronucleus; fp, female pronucleus; A, B, C. Specimens from September; E, F, G, from August.

nomenon was cited for the same species in England by Bass (1979).

Interesting differences also exist between the gametogenesis of *P. amnicum* and *P. dubium* (Say), its vicariant

North American species. In *P. dubium*, oogenesis is a continuous process throughout the year, being more active at the beginning of the summer, but mature ova are present throughout the year. Spermatogenesis in this spe-

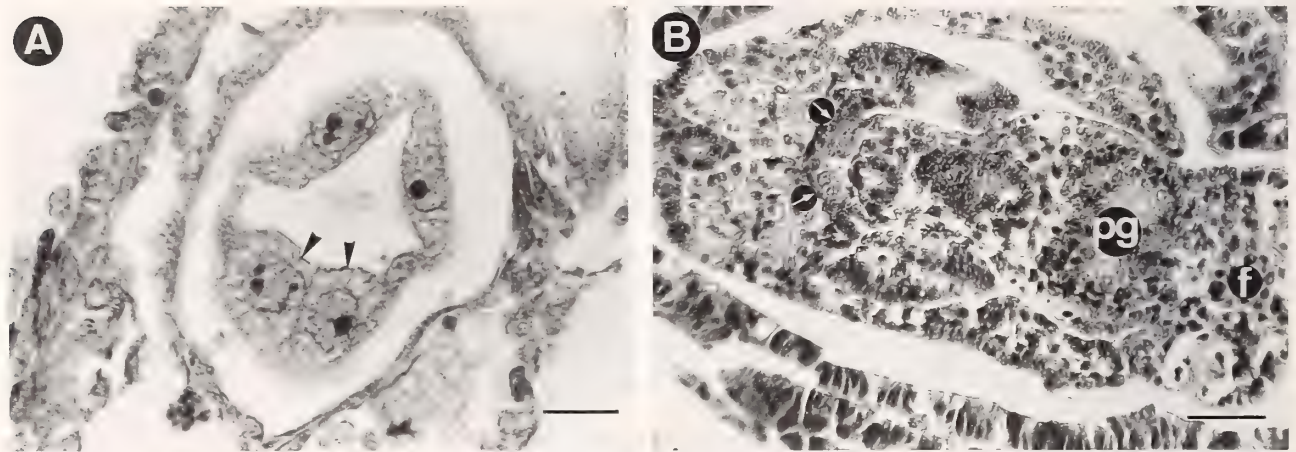


Figure 5

A. Blastula with germ cells (arrow heads). Scale bar = 30 μm . **B.** Prodissoconch larvae with germ cells (arrows). Scale bar = 75 μm . f, foot; pg, pedal ganglia.

cies only occurs in summer, with mature male gametes appearing only during a short period in mid summer (Heard, 1965). Other comparisons between the reproductive strategies of Spanish and other European populations of *P. amnicum* have already been discussed in Araujo et al. (in press). The similarity in the way the testis matures in *P. amnicum* and *Musculium heterodon* is also interesting, as in both species it occurs from the anterior to the posterior region. In the Japanese species, mature spermatozoa are present all year, although a smaller number is observed in winter (Okada, 1935a).

Lucas (1965) proposed that the number of nucleoli differentiates spermatogonia with two nucleoli from oogonia with only one. In the Spanish *P. amnicum* specimens, it was impossible to test this hypothesis because the large amount of chromatin granules in the nucleus of the spermatogonia makes it difficult to determine the number of nucleoli present. Lucas (1965) also cited the difficulty of observing the spermatocyte II due to the speed of the second meiotic division in mollusks. However, we observed this cellular stage in *P. amnicum*, and Okada (1935a) did so in *Musculium heterodon*. Regarding the morphology of the spermatozoa, there are conflicting data in the literature. For Monk (1928) the spermatozoa of *Sphaerium notatum* (Sterki, 1927) lacked a tail, probably due to the difficulty of observing these structures. For Okada (1935a) they were very easy to observe in *Musculium heterodon*. In *P. amnicum*, the tails of the spermatozoa are very difficult structures to identify.

The existence of primary oocytes in spring and autumn in *M. heterodon* (Okada, 1935a) corresponds to the peculiar type of reproduction in this species (and all the Sphaeriinae) in which the embryos are present in the gills of the maternal specimens all year.

According to Okada (1935a), the size of the mature

ovum ("primary oocyte") in *M. heterodon* is about 40 μm , with an eccentric nucleus of 15–20 μm . Woods (1932) illustrated a mature ovum of about 70 μm in *Sphaerium striatinum* (Lamarck), while the maximum size detected in Spanish *P. amnicum* is about 60 μm and corresponds to metaphase I oocytes. Okada (1935a) cited the presence of accessory plasmosomes, a common structure in the nucleus of growing oocytes in mollusks. He suggested that the increase in these structures is transitory due to the increase in nuclear contents; that explains its absence in the first and final stages of oocyte growth. For Stauffacher (1894, in Okada, 1935a), these accessory nucleoli arise from the budding of the main nucleolus. However, in *P. amnicum* these nucleoli are observed in growing and ripe oocytes, and, indeed, in the zygotes recently settled in the gills (Figure 4A), making it difficult to accept such an explanation. As regards the oocyte accompanying cells, our observations also agree with Okada (1935a) in the sense that their relation with the oocyte become less clear as the oocyte grows, supporting Woods' (1932) idea that one or several epithelial cells surrounding the growing oocyte are joined to it, totally or partly, aiding oocyte formation.

No references have been found in other species of *Pisidium* regarding the refringent corpuscles located in the mature female follicles of *P. amnicum*. According to Ituarte (1997), who studied the oosorption process in *Eupera platensis* Doello Jurado, 1921, a South American sphaeriid, the germinal vesicle of degenerative oocytes are not phagocytosed as occurs with the cell cytoplasm; they remain in the lumen of the follicle. Assuming that the corpuscles may be nuclei of degenerated oocytes, this phenomenon could explain their presence in the gonad of *P. amnicum* if other signs of oosorption are found, and their presence indicates a recent spawning process.

Our results suggest that cross-fertilization in *P. amnicum* takes place in the inner gills of the parents, where the meiosis of the ova starts. Nevertheless, Araujo & Ramos (1997), reported and illustrated one specimen in which most of the oocytes, with a diameter between 40–60 μm , had lost the nuclear membrane and appeared in meiotic metaphase inside the ovary. These authors also reported several cases suggesting that intrafollicular fertilization can occur in *P. amnicum*.

Although no gravid specimens appeared among those histologically studied from June and July in this study, some gravid ones were detected by dissections of survivors from a previous cycle (see Araujo et al., in press), suggesting that the fertilization process might begin before August.

ACKNOWLEDGMENTS

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The Eastern Pacific Sportellidae (Bivalvia)

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Abstract. The taxonomy of the eastern Pacific species that have been allocated to the bivalve family Sportellidae is reviewed. All taxa are members of the tropical fauna. The genus *Basterotia* is represented by five species: *B. californica* Durham, 1950, here reported from the Recent fauna for the first time; *B. obliqua* and *B. panamica*, two new species, the latter the most common eastern Pacific species of *Basterotia* and here reported to brood its young; *B. peninsularis* (Jordan, 1936) (of which *B. hertleini* Durham, 1950, and *B. ecuadoriana* Olsson, 1961, are synonyms); and *B. quadrata* (Hanley, 1834) (of which *Poromya granatina* Dall, 1881, is a synonym). The new genus *Basterotina* is described, with the new species *B. rectangularis* as its type species; *Basterotina americana* (Dall, 1900) from the Plio-Pleistocene of Florida is also a member of this genus. *Ensitellops* is represented by *E. hertleini* Emerson & Puffer, 1957 (of which *E. pacifica* Olsson, 1961, is a synonym). *Fabella* is represented by *F. stearnsii* (Dall, 1899) (of which *Sportella duhemi* Jordan, 1936, is a synonym). *Sportella californica* Dall, 1899, is an *Orobitella* (Galeommatoidae: Lasaeidae), and *Anisodonta pellucida* Dall, 1916, is based on a juvenile mactrid, probably *Simomactra falcata* (Gould, 1850).

INTRODUCTION

The Sportellidae is one of four bivalve families currently placed into the Cyamioidea, the others being the Cyamidae (with the Gaimariidae and Perrieriidae regarded as synonyms), the Bernardinidae, and the Neoleptonidae. This complex is much in need of careful analysis to test whether it really represents a clade and whether all of these families, including the Sportellidae, do as well.

The purpose of the present study was to review the eastern Pacific taxa that have been allocated to the Sportellidae. All the species that remain in the family are members of the Panamic fauna, occurring only south of central Baja California. A short summary of the results of this study was presented in the journal of the San Diego Shell Club (Coan, 1997).

Very little is known about the anatomy or ecology of the Sportellidae. Like other cyamioideans, they have posterior incurrent and excurrent openings, but lack or have only very short siphons. There are only four anatomical accounts of genera that have been placed into this family, and one of them seems instead to represent a galeommatid.

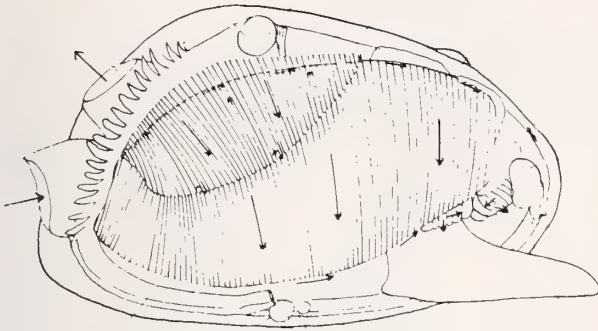
Fischer (1860:23–35, 1886:194) described but did not illustrate the soft parts of *Basterotia quadrata* (Hanley, 1843) (as “*Eucharis*”). Key features mentioned were a mostly fused, strongly papillate mantle, with an oval pedal aperture; separate posterior inhalant and exhalant ap-

ertures, the latter forming a short siphon; ctenidia with two demibranchs, the inner larger; and an elongate, extensible, vertically deployed foot, with a linear groove and pit, presumably for a byssus. This account is probably the source of the information Dall (1899:875) provided about this species.

The poorly known genus *Isoconcha* Pelseneer, 1911, ex Dautzenberg & Fischer ms, was first made available in an anatomical description and figure of its monotypic species, *I. sibogai*. It was described as having a single posterior aperture, a long ventral aperture, and an incomplete anterior inhalent aperture. The foot was described as being pointed and having a strong byssus. The ctenidium had only one demibranch, in which were found incubating eggs (Pelseneer, 1911:47–48, pl. 16, fig. 12, pl. 17, fig. 1; see also Prasad, 1932:173, pl. 9, figs. 9–12). It was placed in the Sportellidae, with question, by Chavan (1969:541), probably because of its entirely external ligament, but its anterior inhalent aperture suggests that a better placement might be the Galeommatidae, close to *Benthoqueta* Iredale, 1930 (type species, by monotypy: *Turqueta integra* Hedley, 1907:364, pl. 66, figs. 7–10), the soft parts of which were studied by Ponder (1968:128–131, figs. 5–7).

Ponder (1971:127, 129–131, figs. 34, 37, 38) described and figured the soft parts of *Anisodonta* (*Tahunanuia*) *alata* (Powell, 1952:170). The inhalent and exhalent openings are posterior, with very short siphons for both. There is a ventral pedal gape. The foot lacks a byssal gland. The inner demibranch is more than twice the size of the outer, and labial palps were figured as being small. Juveniles were found attached to the inside ventral shell margin, each by a single byssal thread (Figure 1).

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Figure 1

Animal of *Anisodonta alata* (Powell), after Ponder (1971).

Finally, Kay (1979:546, fig. 178C; 551; 548, fig. 179L) described and figured the animal of *Basterotia angulata* (Dall, Bartsch & Rehder, 1938) (originally described and in Kay [1979] as "*Anisodonta*")¹. She mentioned a medium-sized foot without a byssus, posterior inhalant and exhalant apertures, the inhalant with a short siphon (opposite to the situation in *B. quadrata*). The inner demi-branch is much larger than the outer (Figure 2).

Unfortunately, nothing is known of the anatomy of living species that have been allocated to *Sportella* (here to *Fabella*).

FORMAT

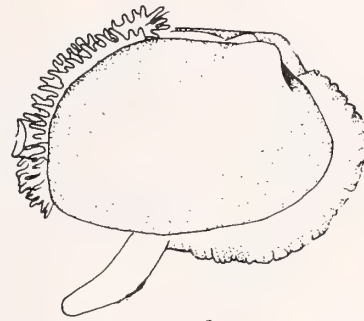
In the following treatment, each valid taxon is followed by a synonymy, information on type specimens and type localities, notes on distribution and habitat, and an additional discussion.

The synonymies include all major accounts about the species, but not most minor mentions in the literature. The entries are arranged in chronological order under each species name, with changes in generic allocation from the previous entry, if any, and other notes given in parentheses.

The distributional information is based on specimens I have examined, except as noted. For many species, the available habitat information is sparse; I have summarized the data available.

References are provided in the Literature Cited for all works and taxa mentioned with dates.

The following abbreviations for institutions and collections are used in the text: ANSP—Academy of Natural Sciences of Philadelphia, Pennsylvania, USA; CAS—California Academy of Sciences, San Francisco, California, USA; LACM—Natural History Museum of Los An-



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Figure 2

Animal of *Basterotia angulata* (Dall, Bartsch & Rehder), after Kay (1979).

geles County, California, USA; MCZ—Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA; MNHN—Muséum National d'Histoire Naturelle, Paris, France; NMW—Naturhistorische Museum, Wien (Vienna), Austria; SBMNH—Santa Barbara Museum of Natural History, Santa Barbara, California, USA; UCMP—University of California Museum of Paleontology, Berkeley, California, USA; UF—Florida Museum of Natural History, University of Florida, Gainesville, Florida, USA; UMML—University of Miami Marine Laboratory (Rosenstiel School of Marine and Atmospheric Sciences), Miami, Florida, USA; USNM—United States National Museum collection, National Museum Natural History, Smithsonian Institution, Washington, DC, USA; Skoglund Coll.—collection of Carol C. Skoglund, Phoenix, Arizona, USA.

DIFFERENTIATING CHARACTERS

A comparative listing of key characters is given in Table 1. A few characters merit additional explanation.

The position of the beaks is given as a percentage of their distance from the posterior to the anterior end. Thus, the beaks of *Ensitellops hertleini* are near the anterior end (80%), whereas those of *Fabella stearnsii* are just posterior to the midline (40%).

The length of the external ligament is given relative to overall shell length. Aside from *Ensitellops hertleini*, which lacks an external ligament, most ligaments are of moderate length (9–13%). Ligaments are short, about 7%, only in *Basterotia quadrata* and *Basterotina rectangularis*.

The internal part of the ligament is generally located on the medial surface of the nymph (no nymph present in *Ensitellops hertleini*). It is fairly broad in *Basterotia californica*, a narrow band adjacent to the external ligament in most taxa, or "small," being restricted to an area near the beaks, as in *B. quadrata* and *Fabella stearnsii*.

¹ A junior homonym but perhaps also a junior synonym of *B. angulata* (H. Adams, 1871:789), originally proposed as *Eucharis*.

The morphology of the hinge teeth are best understood by comparison to the line drawings (Figures 30–42).

The pallial lines are more or less evenly curved in some species (Figures 30, 31, 41, 42), or are deflected toward the postero-ventral margin in most taxa (Figures 32, 34–40).

SYSTEMATIC ACCOUNT

Cyamioidea Sars, 1878:iv, 65²

SPORTELLIDAE Dall, 1899:875

(= Basterotiidae Cossman, in Cossman & Peyrot, 1909:25, 133 [of reprint])

Basterotia Mayer, in Hörnes, 1859

Harlea Gray, 1842:78, genus without named species. Type species: *Corbula quadrata* "Hinds, 1843," by subsequent designation of Smith, 1890:303. *Nomen oblitum*; see Discussion.

Eucharis Récluz, 1850:167. Type species: *Corbula quadrata* "Hinds, 1843," by original designation. *Non Eucharis* Latreille, 1804:175 (Hymenoptera).

Basterotia Mayer, in Hörnes, 1859:71–72. Type species: *B. corbuloides* Mayer, in Hörnes, 1859:71–72, by monotypy. Badenian, Middle Miocene; Mikulov, Czech Republic. (See also Hörnes, 1870:40–41, pl. 3, fig. 11)

Basterotella Olsson & Harbison, 1953:97. Type species: *Pleurodesma floridana* Dall, 1903:1630, pl. 57, fig. 30, by original designation. Late Pliocene or early Pleistocene of Florida.

Discussion: As discussed by Vokes (1981:157, 160), *Harlea* was proposed by Gray (1842) and then resurrected by Smith (1890), but it has never actually been used and is thus a "forgotten name" (*nomen oblitum*). Vokes (1981:157) stated that "the International Commission on Zoological Nomenclature has been requested to suppress the name *Harlea* for purposes of the Law of Priority, but not for the Law of Homonymy," but he evidently never filed a request with the Commission to do so. While a petition to suppress this never-used senior synonym would be called for under the present *Code* (Art. 79), the soon-expected, newly revised *Code* will not require petitions in such clear-cut situations (P. Tubbs, e-mail, 12 June 1997).

As discussed under this species below, the name *Basterotia quadrata* was first made available by Hanley in early 1843, some months before Hinds published it.

Basterotella was differentiated from *Basterotia*, s.s., on the basis that it lacks a sharp angle between the central and posterior slopes, has a longer nymph, and is less pustulose externally. However, the holotype of the type species of *Basterotella*, *Pleurodesma floridana*, has a sharp angle near its umbones as do other specimens I have ex-

amined (UF 9846), and Recent taxa belonging to *Basterotia* have every combination and degree of these three characters. For example, *B. miocenica* Vokes, 1981:161–163, described from the late Lower Miocene Chipola Formation of Florida, was unequivocally assigned to *Basterotella*, but varies from having a rounded to a sharp angle (USNM 298652, 298653, 198654; UF 77588). Little point would thus be served in attempting to allocate the species of *Basterotia* to these two subgenera, leaving either a number of species without subgeneric homes or the subgenera so broadly and complexly defined that they would probably be paraphyletic.

Description: Shell ovate, ovate-elongate, ovate-trapezoidal, to ovate-trigonal; beaks closer to the posterior end, low to inflated. Central slope set off from posterior slope by an angle in some; angle carinate in some. Surface with irregular growth checks, pustulose in most. Right and left valves with projecting anterior cardinals, that in left valve positioned posterior to that of right valve. External portion of ligament of moderate length to very short in some; nymph weak to strong; internal portion of ligament a relatively small, triangular area adjacent to external portion, often extending to a pit under beaks. Left valve often with an escutcheon; right valve either lacking or with a much less conspicuous escutcheon. Pallial line entire.

Carter & Lutz (1990:7, pl. 61) figured the shell structure of the Hawaiian *Basterotia lutea* (Dall, Bartsch & Rehder, 1938:124–125, pl. 34, figs. 7, 8) (as "*Anisodonta*").

Basterotia californica Durham, 1950

(Figures 3–5, 30, 31)

Basterotia californica Durham, 1950:94, 170, pl. 25, figs. 9, 13; Keen, 1971:145 (as a synonym of *B. hertleini*); Bernard, 1983:33 (as a synonym of *B. hertleini*)

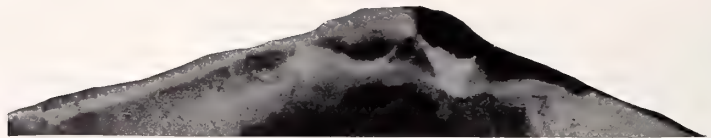
Type material and locality: UCMP 32668, holotype, left valve, now lost; length, 8.5 mm; height, 4.9 mm; thickness, 1.7 mm (Figure 3a, b). UCB Loc. A3582; Bahía Santa Inez, Baja California Sur (27.1°N, 112.0°W); "from 20-foot terrace level extending from Loc. A3581 to beach"; Pleistocene. (Loc. A3581; W. of Punta Santa Inez, about 0.5 miles from beach, at end of hill; Lower Pliocene).

Description: Shell ovate-elongate, length/height about 1.6; beaks at approximately 60–70% of distance to anterior end; anterior end rounded; posterior end subtruncate, tilted anteriorly approximately 20° from vertical. Central slope set off from posterior slope by only a rounded angle. Surface with strong, irregular commarginal growth checks, without conspicuous pustules. Right valve with an elongate, vertical to slightly anteriorly directed, projecting anterior cardinal, and a small, horizontal process attached to it dorsally; left valve with an oblique, projecting, horizontally elongate anterior cardi-

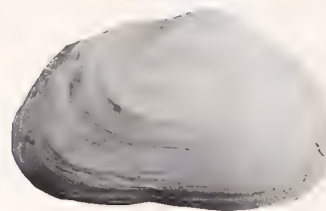
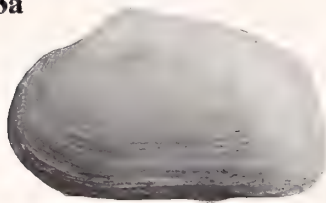
² Chavan (1969:537) and Ponder (1971:125) credit this family-level name to Philippi (1845), but I find only the genus *Cyamium* in Philippi (1845:50–51). As far as I have been able to discover, Sars (1878) is the earliest author to use this name.



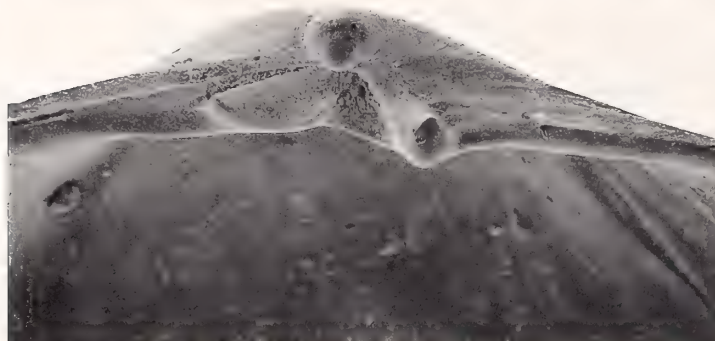
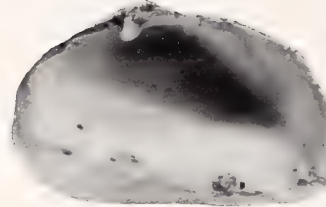
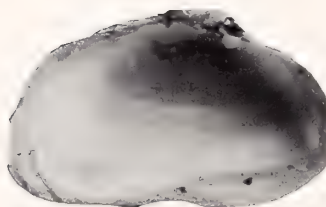
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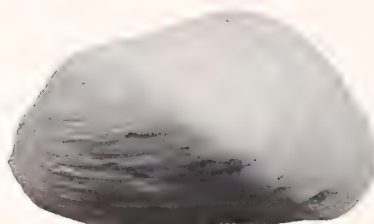
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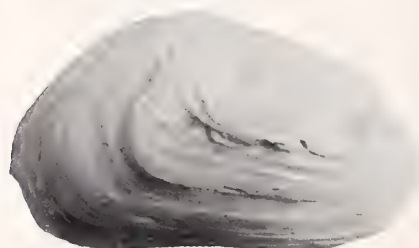
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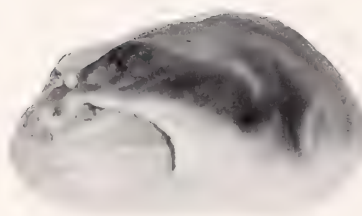
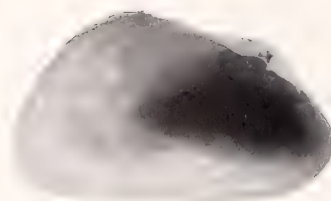
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nal, and a conspicuous gap under beaks for cardinal of right valve. External portion of ligament of moderate length, separated from internal portion by a ridge; nymph weak; internal portion wide, extending into a pit under beaks. Pallial line even curved, not deflected toward posteroventral corner. Left valve with an elongate escutcheon; escutcheon weaker, most visible posteriorly in right valve. Length to 12.5 mm (SBMNH 143609; Bahía San Luis Gonzaga, Baja California [Norte]). Additional specimens are illustrated here (Figures 4, 5, 30, 31).

Distribution: Northeastern end of Isla Cedros, Baja California [Norte] (28.3°N) (LACM 71-152.30), in the Golfo de California from Los Frailes, Baja California Sur (23.4°N) (Skoglund Coll.), north to Bahía Cholla, Sonora (27.9°N) (Skoglund Coll.), south on the Sonoran coast to Bahía San Carlos (27.9°N) (LACM 78-30.10), Mexico. There are records from the intertidal zone to 100 m (mean, 26 m); the only bottom type noted is sand. There are only two live-collected specimens, SBMNH 144173, from 30 m, and SBMNH 143609, for which no habitat information is available. I have seen 29 Recent lots. Also present in the Pleistocene near Bahía Santa Inez, Baja California Sur (type locality).

Discussion: It is unfortunate that the unique holotype of this species has been lost, but the original description and illustrations are sufficient to permit its recognition as a distinct species that is also represented in the Recent fauna of northwest Mexico.

It is most similar to *Basterotia peninsularis*, differing in the following respects: (1) the beaks are closer to the midline; (2) the dorsal and ventral margins are more parallel; (3) the pallial line is more evenly curved, lacking the sharp bend toward the posteroventral margin present in *B. peninsularis*; and (4) the anterodorsal shell margin is not flared and pustulose, as it generally is in *B. peninsularis*. The hinge also differs significantly: the external portion of the ligament is proportionately longer in *B. californica*, the nymph is less conspicuous, and the internal portion extends over a broader, more triangular area. In the right valve, the base of the large cardinal tooth is broader in *B. californica*; in the left valve, the cardinal tooth is more horizontal and less projecting. Juveniles of *B. californica* tend to be proportionately thicker-shelled and those of the other species.

Basterotia obliqua, Coan, sp. nov.

(Figures 6, 7, 32, 33)

Type material and locality: LACM 2846, holotype, left valve; length, 9.0 mm; thickness, 2.2 mm (Figures 6, 32); LACM 2847, paratype, right valve; length, 10.1 mm; height, 6.2 mm (Figures 7, 33); LACM 2848, paratype, left valve, length, 8.4 mm. LACM 78-30, 3 mi. S. of Las Tetas de Cabra, Bahía San Carlos, Mexico (27.9°N, 111.1°W); 100 m on bottom of shells, cobbles and silt; Roy & Forest Poorman, April 1978.

Description: Shell ovate-oblique, thin; length/height about 1.6; beaks approximately 75–80% of distance to anterior end; anterior end narrowed, rounded; posterior end broad, subtruncate, tilted anteriorly about 30° from vertical; dorsal margin oblique to ventral margin; central slope set off from posterior slope by an obscure angle only near beaks. Surface with irregular commarginal growth checks; pustules sparse, restricted to dorsal and anterior margins in some specimens. Right valve with a narrow, projecting, peglike cardinal; left valve with a narrow, not very projecting cardinal and a gap for cardinal of right valve under beaks. External portion of ligament of moderate length for genus, not separated from internal portion; nymph heavy; internal portion of ligament small, restricted to medial surface of nymph. Pallial line deflected toward posteroventral corner. Left valve with a conspicuous, elongate escutcheon; escutcheon present but less evident in right valve. Length to 10.7 mm (Skoglund Coll.; Los Frailes, Baja California Sur).

Distribution: Type lot, see above (27.9°N); Known from only four lots, from 16–100 m (mean, 57 m): Skoglund Coll.—Los Frailes, Baja California Sur (23.4°N); 50–66 m; left valve; LACM 34-20.13—Caleta Tagus, Isla Isabela, Islas Galápagos (0.3°S); 55 m; rock/coral bottom; small, broken left valve; LACM 34-61.16—Bahía Cartago, Isla Isabela, Islas Galápagos (0.6°S); 15–18 m; sand; left valve.

Discussion and comparisons: This species differs from *B. peninsularis* in being trapezoidal rather than oval, thinner shelled, in lacking a produced anterodorsal margin, having narrower beaks, and a sharper angle between the posterodorsal and central slopes. In shape, it is closer to *B. panamica*, but it is thinner, more trapezoidal, and it

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Explanation of Figures 3–7

Figures 3–5. *Basterotia californica*. Figure 3a, b. Holotype, now lost; length, 8.5 mm. Figure 4. Pair, SBMNH 143609; Bahía San Luis Gonzaga, Baja California [Norte]; about 6 m; length, 10.0 mm. Figure 5. Left valve, close-up of hinge; SBMNH 143609; shell length, 5.5 mm. Figures 6, 7. *Basterotia obliqua*, Coan, sp. nov. Figure 6, holotype, left valve; LACM 2846; length, 9.0 mm. Figure 7, paratype, right valve; LACM 2847; length, 10.1 mm.

has a narrower escutcheon and a thinner hinge. *Basterotia obliqua* differs from *B. oblonga* Smith, 1890 (pp. 303–304, pl. 22, fig. 5), from St. Helena in having a more pronounced angle between the posterior and central slopes near the beaks and a heavier nymph. It differs from *B. lutea* (Dall, Bartsch & Rehder, 1938) from Hawaii in having a longer ligament.

Etymology: The name is derived from the oblique shape of the shell of this species.

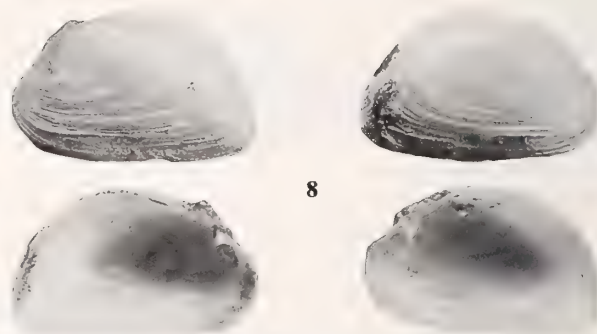
Basterotia panamica Coan, sp. nov.

(Figures 8–10, 34)

?*Basterotia peninsularis* (Jordan), auctt. non Jordan, 1936 (see Discussion under *B. peninsularis*). Durham, 1950: 95, 170; pl. 25, figs. 3, 8; Keen, 1958:106, 107, fig. 218 (in part); Keen, 1971:145, 146, fig. 342 (in part)

Type material and locality: SBMNH 144168, holotype, complete pair; length, 7.3 mm; height, 4.5 mm; thickness, 3.5 mm (right valve slightly broken on posterodorsal margin) (Figures 8, 34). SBMNH 144169, paratypes, four pairs containing dried animals, 8.1 mm, 7.7 mm, 7.4 mm, 7.4 mm in length. SBMNH 144170, paratypes, two pairs with dried animals, 8.1 mm, 6.9 mm in length. “Tecuan,” Jalisco, Mexico (19.3°N, 104.9°W); in estuary mouth under rocks at low tide; Carol C. Skoglund, December 1974.

Description: Shell ovate-trapezoidal, length/height about 1.6; beaks approximately 85% of distance to anterior end; anterior end rounded; posterior end subtruncate, tilted anteriorly about 30° from vertical; central slope generally set off from posterior slope by an angle, varying among lots from rounded to sharp to carinate (angle moderate in type lot). Entire surface with dense fine to coarse granules and with strong, irregular commarginal growth checks. Right valve with an elongate, projecting, nearly vertical anterior cardinal and an obscure, short, thick horizontal process attached to it dorsally; left valve with a narrow, vertically elongate, projecting anterior cardinal and a conspicuous gap medial to it for cardinal of right valve. Ligament of moderate length, its external portion on a nymph of moderate strength, slightly divided from its internal portion, which is narrow to medium in width and extends across anterior end of nymph into a pit under beaks. Pallial line deflected toward posteroventral corner. Conspicuous escutcheon present in left valve, smaller or inconspicuous in right valve. When valves closed, anterior and ventral margins gaping, the ventral margin gaping two-thirds of distance to posterior slope. Mantle with a short pedal gape. Posterior end with incurrent and excurrent openings, without siphons (openings very small in dried material). This species broods its young along its ventral mantle margin (Figure 10). Length to 11.0 mm (LACM 71–177.30; Punta San Pablo, Baja California Sur), 10.5 mm (SBMNH 144172; south end of Isla San Marcos,



10

Explanation of Figures 8–10

Figures 8–10. *Basterotia panamica* Coan, sp. nov. Figure 8, holotype, pair; SBMNH 144168; length, 7.3 mm. Figure 9. Left valve, close-up of hinge; SBMNH 144171; Bahía San Luis Gonzaga, Baja California [Norte]; about 6 m; length, 6.2 mm. Figure 10. Brood on ventral margin of mantle in a left valve; SBMNH 143659, Cabo San Lucas, Baja California Sur; 12 m; adult shell length, 10.5 mm; juveniles, approximately 0.2 mm.

Baja California Sur). An additional specimen is illustrated here (Figure 9).

Distribution: Punta San Pablo, Baja California Sur (27.2°N) (LACM 71–177.30, a single right valve with a

broken hinge, the only specimen seen from the Pacific coast of Baja California), into the Golfo de California as far north as Bahía Cholla, Sonora (31.4°N) (SBMNH 14366; Skoglund Coll.), south along the coasts of Mexico and Central America to Salinas, Guayas Province, Ecuador (2.2°S) (CAS 106168), and in the Islas Galápagos at eight stations: Isla Genovesa (0.3°N) (CAS 106384); Isla Isabela (0.3°S) (CAS 106379); Isla Baltra (0.4°S) (LACM 34-46.1); Isla Santa Cruz (0.5°S) (ANSP 154907); Isla Santa Cruz (0.8°S) (CAS 106153); Isla San Cristóbal (0.8°S) (LACM 34-43.20); Isla San Cristóbal (0.9°S) (MNHN); Isla Española (1.4°S) (CAS 106153; LACM 34-283.7).

This species occurs from the intertidal zone to 119 m (mean, 20 m). Live-collected material has been obtained from the intertidal zone to 11 m. Various bottom types are noted on labels, including mud, sand, and rubble; however, live collected material was obtained under rocks, suggesting a nestling habitat. I have seen 82 Recent lots. Perhaps in the Pleistocene of the southern Golfo de California (see Discussion under *B. peninsularis*).

Discussion and comparisons: This new species differs from *Basterotia peninsularis* in having a more trapezoidal outline, with a shorter, narrower, more ventrally positioned anterior end and a broader, more truncate posterior end. Its surface is lightly to coarsely pustulose, whereas that of *B. peninsularis* is scarcely pustulose, with pustules chiefly restricted to the antero- and posterodorsal margins. The posterior slope of this new species is separated from the central slope by an angle, which may be sharp or even carinate in some material; there is no such angle in *B. peninsularis*. In the right valve, the small horizontal process dorsal to the cardinal tooth is much less conspicuous; in the left valve, the large cardinal projects more dorsally. The external and internal portions of the ligament of the new species are not separated by a conspicuous ridge medially, as they are in *B. peninsularis*.

The poorly known *Basterotia pustula* Nowell-Usticke, 1971 (pp. 29-30, pl. 5, fig. 1618), described from St. Croix, Virgin Islands, differs in being thinner and more elongate.

Material from the southern end of the distribution of this species is more consistently carinate between the central and posterior slopes and is also more variable. Eventually, this southern material may be found to be taxonomically distinct.

The brooding in this species along the mantle margin is similar to that described for *Anisodonta alata* (Powell, 1952), by Ponder (1968).

Etymology: The name is derived from the Panamic province, in which this is the most common species of *Basterotia*.

Basterotia peninsularis (Jordan, 1936)

(Figures 11-15, 35, 36)

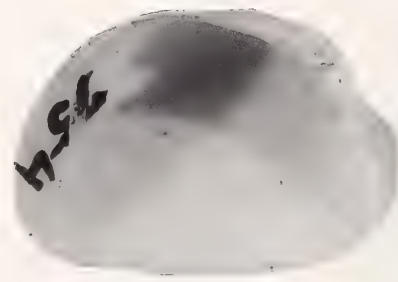
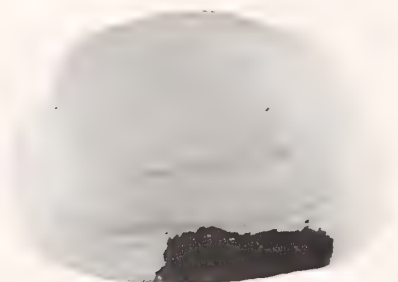
Anisodonta peninsulare Jordan, 1936:147, pl. 18, figs. 11, 12; (the following references all as *Basterotia*); Durham, 1950:95 (in part), not pl. 25, figs. 3, 8; Hertlein & Strong, 1947:137; Keen, 1958:106 (in part), not 107, fig. 218; Keen, 1971:145 (in part), not 146, fig. 342; Bernard, 1983:33.

Basterotia hertleini Durham, 1950:94-95, 170, pl. 25, figs. 4, 11; Emerson & Hertlein, 1964:355, 357, 358, 359, fig. 4g-j; Keen, 1971:145, 146, fig. 343; Hertlein & Grant, 1972:241-242, pl. 57, figs. 6, 11; Bernard, 1983:33.

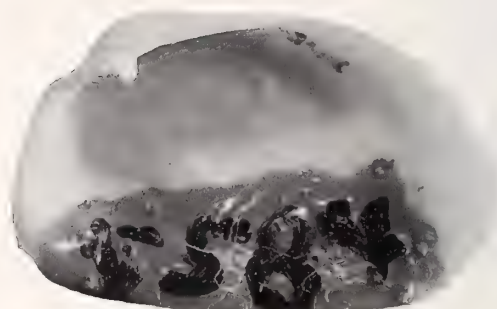
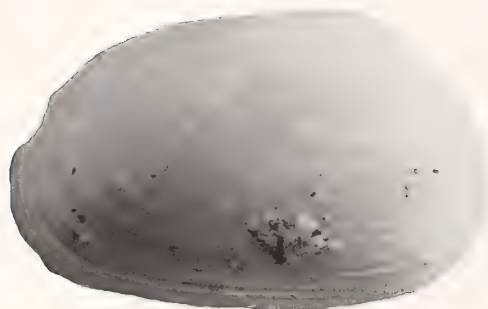
Basterotia ecuadoriana Olsson, 1961:243, 509, pl. 36, fig. 8, 8a; Keen, 1971: 145 (as a synonym of *B. hertleini*); Bernard, 1983:33 (as a synonym of *B. hertleini*).

Type material and localities: *A. peninsulare*—CASGTC 754.05 (originally 5583), holotype, left valve; length, 15.0 mm; height, 10.6 mm; thickness, 3.8 mm (Figure 11). CAS 754.06 (originally 5584), paratype, right valve; length, 11.2 mm (Figure 12). CAS Loc. 754, north of village, Bahía Magdalena, Baja California Sur (24.6°N, 112.2°W); Pleistocene. *B. hertleini*—UCMP 32274, holotype, left valve; length, 13.2 mm; height, 7.6 mm; thickness, 3.6 mm (Figure 13); UCMP 32328, paratype, left valve; length, 11.5 mm; UCMP 32372, paratype, right valve; length, 10.0 mm; CAS 8581, paratype, right valve; length, 9.9 mm; CAS 8581a, paratype, left valve; length, 11.5 mm. CAS 8581b, paratype, right valve; length, 8.5 mm. UCB Loc. A3670, Puerto Balandra, Isla Carmen, Baja California Sur (26.0°N, 111.2°W); Upper Pliocene; "from sands at left end of outcrop and below base of coral reef." There were also said to be specimens from UCB Locs. A3519 and A3520; Bahía Marquer, Isla Carmen; Upper Pliocene. *B. ecuadoriana*—ANSP 218892, holotype, left valve; length, 12.3 mm; height, 7.7 mm; thickness, 2.3 mm (Figure 14). Manta, Manabi Province, Ecuador (0.1°S, 80.8°W). Paratype, left valve, length, 15.2 mm, not located. Punta Santa Elena, Guayas Province, Ecuador (2.2°S, 81.0°W).

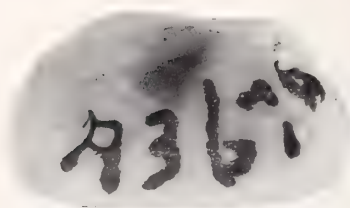
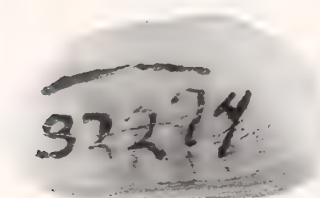
Description: Shell ovate to ovate-trapezoidal; length/height about 1.7; beaks approximately 75% of distance to anterior end; anterior end rounded; posterior end subtruncate, tilted anteriorly about 30° from vertical; anterodorsal margin often somewhat flared; dorsal margin often denticulate; central slope set off from posterior slope by only a rounded angle. Surface with irregular commarginal growth checks; pustules, if present, sparse, restricted to small specimens and along dorsal margin of larger specimens. Right valve with a projecting, elongate, vertical anterior cardinal and with a very small anteroposteriorly elongate process attached to it dorsally; left valve with a narrow, vertical, projecting cardinal and a gap under beaks for cardinal of right valve. External portion of ligament of moderate length for genus, separated from internal portion by a ridge; nymph of moderate strength;



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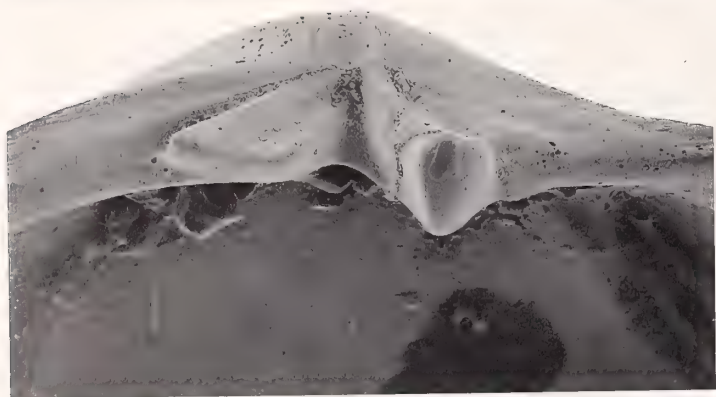
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internal portion of ligament narrow, often with a pit under beaks. Pallial line deflected toward posteroventral corner. Left valve generally with an inconspicuous escutcheon; escutcheon absent or much less evident in right valve. Length to 18.7 mm (MNHN; Punta Santa Elena, Guayas Province, Ecuador). Additional specimens are figured here (Figures 15, 35, 36).

Distribution: From Isla Espíritu Santo, Baja California Sur (24.5°N) (CAS 106155), north in the Golfo de California to Bahía Cholla, Sonora (31.4°N) (Skoglund Coll.), Mexico, south to Salinas, Guayas Province, Ecuador (2.2°S) (MNHN; ?CAS 110366), and in the Islas Galápagos on Isla Isabela (0.2°S) (LACM 34–30.11) and Isla Baltra (0.4°S) (LACM 34–46.28). Specimens have been obtained from the intertidal zone to 46 m (mean, 16 m); all material has been obtained dead. I have examined 40 Recent lots. The bottom type most often noted is sand, but some labels mention mud or rocks. Also know from the Pliocene of southern California (Hertlein & Grant, 1972) and of the islands in the southern Golfo de California (Durham, 1950; Emerson & Hertlein, 1964) and the Pleistocene of Bahía Magdalena, Baja California Sur (Jordan, 1936).

Discussion: The holotype of *Anisodonta peninsulare* is a very large, oval specimen of the same species that was later named *Basterotia hertleini*. The paratype of *A. peninsulare* is a more typical specimen and is similar to the holotype of *Basterotia hertleini*. The material referred to and illustrated as *B. peninsularis* by Durham (1950) consists of specimens that are strongly carinate and heavily pustulose—UCMP 32271, 32272, 32273; CAS 66787.01; SBMNH 143667—all from UCB loc. A3548; Pleistocene; Isla Coronados, Baja California Sur (26.1°N). These specimens are morphologically intermediate between *B. quadrata* (see below) and *B. panamica*. They are thicker-shelled and more regular in shape than *B. quadrata*, and they have a longer ligament and nymph. On the other hand, they are larger than any known specimens of *B. panamica*; the largest is 13.9 mm in length, and the specimen figured by Durham (1950) is 12 mm in length. Durham's figures were then reproduced in Keen (1958, 1971), forming a mistaken concept of *B. peninsulare* among students of the Recent Panamic fauna. These Pleistocene specimens may be assignable to *B. panamica*,

or they may represent an evolutionary stage on the way to it.

Basterotia ecuadoriana has been generally been synonymized with *B. hertleini*. Olsson differentiated his new species from *B. hertleini*, saying that *B. ecuadoriana* differed in being more elongate and less convex. In actuality, the holotype of *B. hertleini* has a length/width ratio of 1.7, whereas the holotype of *B. ecuadoriana* has a ratio of 1.6. On the other hand, the holotype of *B. ecuadoriana* is indeed flatter, with a thickness/height ratio of 0.3, whereas the holotype of *B. hertleini* has a ratio of 0.5. In any event, these differences are within the range of variability of *B. peninsularis*.

For comparisons with *B. californica*, see under that species. *Basterotia peninsularis* is most similar to the western Atlantic *B. elliptica* (Récluz, 1850:168–169) (synonym: *Corbula newtoniana* C. B. Adams, 1852:240), which differs in being proportionately shorter, more ovate-trapezoidal, in having a shorter, less produced anterior end, and in lacking a denticulate dorsal margin. It also has a still shorter external ligament.

The western Atlantic *Basterotia corbuloidea* (Dall, 1899:885–886, 896, pl. 88, fig. 2, as *Anisodonta*)³ is smaller and thinner, and its beaks are closer to the anterior end.

Basterotia quadrata (Hanley, 1843)

(Figures 16–18, 37, 38)

Corbula quadrata Hanley, 1843 (early 1843):7, pl. 12, fig. 36; Hinds, 1843 (Nov.):57; Reeve, 1844:pl. 5, fig. 40; Récluz, 1850:168 (*Eucharis*); C. B. Adams, 1852:239–240 (*Corbula*); Hanley, 1856:345 (*Corbula*); Fischer, 1860:23–26 (*Eucharis*); Fischer, 1886:199 (*Eucharis*); Dall, 1899:875, 877 [*Anisodonta* (*Basterotia*)]; Lamy, 1925:505; Olsson, 1961:242 [*Basterotia* (*Basterotia*)]; Bernard, 1983:33, 68 (as “extralimital” to the eastern Pacific).

Poromya (?) *granatina* Dall, 1881:109; Dall, 1886:316, pl. 1, fig. 2, 2a, 2b (as *Basterotia quadrata* var. *granatina*); Lamy, 1925:506 (as a variety of *B. quadrata*).

Type material and localities: *C. quadrata*—Original specimens missing (K. Way, e-mail, 18 September 1996).

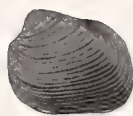
³ Not a homonym and not to be confused with the type species of the genus, *Basterotia corbuloides*.

Explanation of Figures 11–15

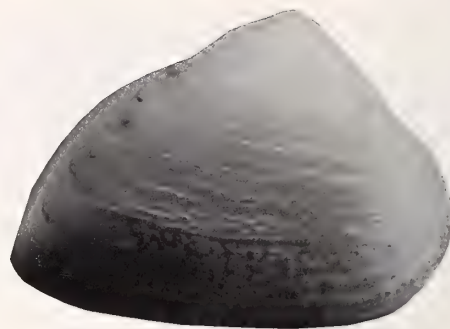
Figures 11–15. *Basterotia peninsulare*. Figure 11. Holotype of *Anisodonta peninsulare*, left valve; CASGTC 754.05; length, 15.0 mm. Figure 12. Paratype of *A. peninsulare*, right valve; CASGTC 754.06; length, 11.2 mm. Figure 13. Holotype of *Basterotia hertleini*, left valve; UCMP 32274; length, 13.2 mm. Figure 14. Holotype of *Basterotia ecuadoriana*, left valve; ANSP 218892; length, 12.3 mm. Figure 15. Left valve, close-up of hinge; SBMNH 143606; Bahía San Luis Gonzaga, Baja California [Norte]; about 6 m; shell length, 8.8 mm.



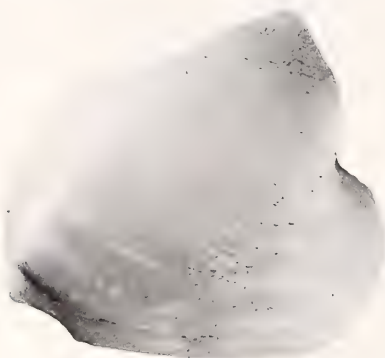
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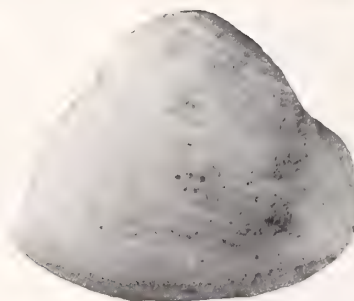
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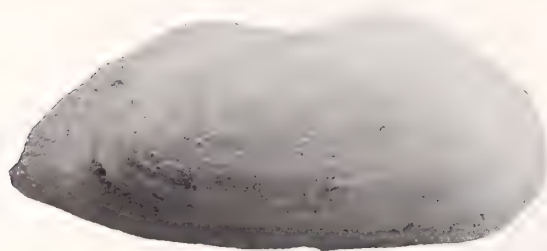
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Hanley's figure measures 9 mm in length and 8 mm in height (Figure 16). Hinds gives the length of his specimen as 6 lines (12.7 mm) and its height as 5 lines (10.6 mm) (Figure 17). Original locality unknown. *P. granatina*—MCZ 8133, holotype, right valve; length, 9.9 mm; height, 6.8 mm; thickness, 3.2 mm (Figure 18). Yucatan Strait; "off Cuba" (a label); 640 fms. (1170 m, probably much too deep to reflect its true habitat).

Description: Shell ovate-trigonal, length/height about 1.1; beaks approximately 70% of distance from anterior end, very prominent, inflated, and strongly prosogyrate in some material; anterior end rounded; posterior end rounded to subtruncate, inclined anteriorly about 30° from vertical; central slope divided from posterior slope by a 90° angle near beaks; angle with a carina, most prominent dorsally, broadening toward ventral margin. External surface with coarse pustules and heavy, irregular commarginal growth checks. Posterodorsal margin pustulose. Right valve with a prominent, ventrally projecting cardinal; left valve with a prominent, projecting cardinal. External portion of ligament very short, on a short, sturdy nymph; internal portion small, on medial surface of nymph, extending to a pit under beaks. Narrow to wide escutcheon present in left valve; escutcheon not present in right valve. Pallial line not greatly deflected toward posteroventral margin. Length to 14.1 mm (MNHN; Salinas, Guayas Province, Ecuador). Additional eastern Pacific specimens are illustrated here (Figures 19, 20, 37, 38).

Distribution: In the eastern Pacific, from near Isla Partida, Baja California Sur (24.5°N) (LACM 60-6.24), throughout the Golfo de California to its head at Bahía Cholla, Sonora (31.4°N) (Skoglund Coll.), south to Salinas, Guayas Province, Ecuador (2.2°S) (MNHN), and in the Islas Galápagos on Isla Isabela (0.3°S) (CAS 110365) and Isla Santa Cruz (0.5°S) (ANSP 400163). Stations are from 6 to 119 m (mean, 28 m). No bottom types were noted. I have seen 13 Recent eastern Pacific lots. Also present on the Pleistocene 3rd Terrace at Punta Santa Elena, Guayas Province, Ecuador (Hoffstetter, 1948:75; MNHN).

In the western Atlantic, from Cape Lookout, North Carolina (34.3°N) (USNM 94210), on both coasts of Florida, in the Bahamas (C. Redfern, in correspondence, 3

April 1997), south to Haiti (USNM 440430 and other lots), Guadalupe (MNHN), and Colombia (UCMP S-10).

Discussion: Although overlooked by previous workers, this species was first proposed in Hanley (1843), which was published early in the year, many months before the name was made available by Hinds (1843) (see Literature Cited for collation of Hanley). While Hanley's figure, an external view, is not unequivocal, interpreting *Corbula quadrata* Hanley as a *nomen dubium* would only create a senior homonym of *Corbula quadrata* Hinds.

Specimens of this species from the eastern Pacific are indistinguishable from those from the Caribbean. This species differs from the very similar *Basterotia* (*Basterotia*) *ambona* Vokes, 1981:160–161, 163, figs. 1–3, described from the late Lower Miocene Chipola Formation of Florida, in having a more expanded, denticulate posterodorsal margin; in *B. ambona*, it is more evenly curved and is not denticulate. In the Recent taxon, the posteroventral corner is more pointed, and the hinge teeth seem somewhat broader (material of *B. ambona* examined: USNM 298649, 298650, 298651; UF 77591). Indeed, *B. quadrata* is very close to the Middle Miocene type species of the genus, *B. corbulides*, differing in having a denticulate posterodorsal margin, a more curved ventral margin, and on average a slightly more produced anterior end, and in lacking a depressed area just anterior to the carina, which is in part responsible for the straighter ventral margin, and perhaps in attaining a larger size (material of *B. corbuloides* examined: NMW 1855/XLV/282, 2 paratypes).

Dall (1886:316) cited this species from the Pacific coast, but there are no eastern Pacific specimens in the USNM. His record was repeated with question by Olsson (1961:242) and then dismissed by Bernard (1983:33, 68). However, as can be seen, it does indeed occur in the eastern Pacific in addition to the western Atlantic. Dall (1886:316) also mentioned seeing possible material of this species from Korea. I suspect, however, he may have seen specimens of the Indo Pacific *Basterotia angulata* (H. Adams, 1871:789, 795, pl. 48, fig. 3) (*Eucharis*), which differs from *B. quadrata* in being more elongate and having a longer external ligament, and it has no tendency to form greatly expanded, prosogyrate beaks. *Basterotia angulata* (H. Adams, 1871) is a senior homonym

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Explanation of Figures 16–22

Figures 16–20. *Basterotia quadrata*. Figure 16. Hanley's (1843) figure; length, 9 mm. Figure 17. Reeve's (1844) figure, probably of Hinds' specimen; length, 12.7 mm. Figure 18. Holotype of *Poromya granatina*, right valve; MCZ 8133; length, 9.9 mm. Figure 19. Right valve; SBMNH 143655; Puerto San Carlos, Sonora, Mexico; 27 m; length, 12.5 mm. Figure 20. Right valve; LACM 72-54.46; Bahía Herradura, Puntarenas Province, Costa Rica; 37 m; length, 9.6 mm. Figures 21–22. *Basterotina rectangularis* Coan, gen. & sp. nov. Figure 21. Holotype, right valve; SBMNH 144174; length 11.0 mm. Figure 22. Paratype, left valve; SBMNH 144175; length 7.8 mm.



23a



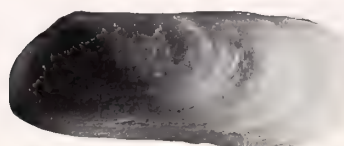
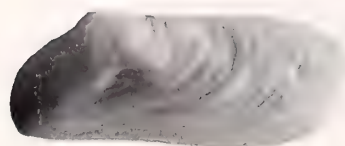
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of *B. angulata* (Dall, Bartsch & Rehder, 1938:125, pl. 34, figs. 5, 6) (*Anisodonta*); however, because it may also be a senior synonym of this Hawaiian taxon, it may not need to be renamed.

***Basterotina*, Coan, gen. nov.**

Type species: *B. rectangularis* Coan sp. nov.

Description: Shell subquadrate; beaks at 70% from posterior end; posterior end truncate; central and posterior slopes separated by an angle, often carinate; surface pustulose. Hinge teeth not projecting, as in *Basterotia*. Right valve with a moderate to obscure cardinal, attached dorsally to an obscure, anteroposteriorly oriented process; left valve with an anterior cardinal formed by hinge margin, fitting anterior to cardinal of right valve. External portion of ligament in a groove, strengthened by a weak nymph most evident posteriorly; internal ligament in an elongate, triangular area. Escutcheon most apparent in left valve. Posterior margin of anterior adductor muscle scar with a radial strengthening rib.

Discussion and comparisons: This genus differs from *Basterotia* in having low, non-projecting hinge teeth, but is similar to many species of that genus in having the posterior and central slope separated by an angle and in being pustulose. It differs from the type species of *Anisodonta* Deshayes, 1858:542–543, *A. complanata* Deshayes, 1858:543, pl. 22, figs. 1–4, from the Paleocene of France, in being carinate and pustulose, and in having a greater amount of internal ligament, but is similar in having an internal thickening posterior to the anterior adductor (material of *A. complanata* examined: Senckenberg Museum).

In addition to the following species, *Anisodonta americana* Dall, 1900, from the Miocene of Florida, also belongs in this genus (see additional comparison below).

Etymology: The name of this genus is derived from *Basterotia*, suggesting its probable relationship to this genus, with the addition of the diminutive, *-ina*.

***Basterotina rectangularis* Coan, sp. nov.**

(Figures 21–23, 39, 40)

Type material and locality: SBMNH 144174, holotype, right valve; length, 11.0 mm; height, 5.1 mm; thickness,

2.0 mm (Figures 21, 40). SBMNH 144175, paratype, left valve; length, 7.8 mm (Figures 22, 39). Los Frailes, Baja California, Sur (23.4°S, 109.4°W); 60 m; Pete & Iva Barker, February 1973; *ex* Skoglund Collection.

Description: Shell elongate-rectangular, length/height 2.5; beaks approximately 70% of distance to anterior end; anterior end rounded; posterior end broad, truncate, tilted anteriorly about 40° from vertical; posterodorsal margin slightly concave; central slope set off from posterior slope by an angle, which may be carinate in some material. Surface coarsely pustulose, most conspicuously on ends, and with irregular commarginal growth checks. Right valve with an obscure, slightly anteriorly directed, non-projecting anterior cardinal, with a small, anteroposteriorly elongate process dorsal to it; left valve with a small, slightly projecting anterior cardinal formed by hinge margin. External portion of ligament elongate, on a conspicuous nymph; internal portion narrow, separated from external portion by an obscure ridge. Pallial line deflected toward posteroventral corner. Left valve with a well-defined escutcheon; right valve without one. Anterior adductor muscle scars with a posterior strengthening rib. Length to 11.0 mm (holotype). Two additional specimens are illustrated here (Figure 23).

Distribution: East side of Isla Cedros, Baja California [Norte] (28.2°N) (LACM 71–94.27), into the Golfo de California as far north as near Bahía Puertecitos, Baja California [Norte] (30.4°N) (LACM 72–215.19), and Bahía San Carlos, Sonora (27.9°N) (LACM 78–30.9), south to the north side of Isla Salango, Manabi Province, Ecuador (1.6°S) (LACM 80–65.9), from 9 to 100 m (mean, 47 m). The only bottom type noted on labels was sand. This species is thus far known from only eight lots, all obtained dead.

Other referred material: CAS 106154—“Gulf of California,” Mexico; Skoglund Coll. - Punta San Antonio, Sonora, Mexico; SBMNH 143656 - Bahía Las Palmas, Baja California Sur, Mexico.

Discussion and comparisons: This species is most similar to *Basterotina americana* (Dall, 1900:1133, pl. 36, fig. 7; USNM 107808, holotype, right valve) (*Anisodonta*), described from the Caloosahatchee Formation of Monroe County, Florida (late Pliocene or early Pleistocene) and subsequently also figured from beds of similar

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Explanation of Figures 23–26

Figure 23. *Basterotina rectangularis* Coan, gen. & sp. nov. (a) Left and (b) right valves, close-up up of hinges; LACM 71–94.27; E. of Isla Cedros, Baja California [Norte]; about 24 m; right valve length, 5.8 mm; left valve length, 4.4 mm. Figures 24–26. *Ensitellops hertleini*. Figure 24. Holotype of *E. hertleini*, left valve; UCMP 11243; length, 8.5 mm. Figure 25. Holotype of *E. pacifica*, left valve; ANSP 218893; length, 5.4 mm. Figure 26, three left valves, showing variability; LACM 40–50.31; Bahía Topoca, Sonora, Mexico; 7.4, 7.4, 7.0 mm.

age at Shell Creek, Florida (Dall, 1903:pl. 57, fig. 23). The Recent species differs in being more elongate, less produced and angled posterodorsally, and more oblique posteriorly; the posterior end of *B. americana* is tilted only about 20–30° from vertical. The ventral margin of the anterior hinge plate in the right valve is not as recessed in the Recent species as it is in *B. americana*, in which this margin forms a slot, and the nymph is less conspicuous, as are the hinge teeth. The thickening posterior to the anterior adductor muscle scar is heavier in *B. americana*.

Etymology: The name is derived from the rectangular shape of the shell of this species.

Ensitellops Olsson & Harbison, 1953

Ensitellops Olsson & Harbison, 1953:93. Type species: *Sportella protexta* Conrad, 1841:347. Pliocene; North Carolina. (Concerning this species: Campbell, 1993:33, pl. 10, fig. 99.)

Description: Shell very elongate, flattened to somewhat inflated, thin, fragile; beaks closer to the posterior end. Surface with irregular commarginal growth checks and scattered pustules. Right valve with a single vertical to anteriorly directed cardinal; left valve with anterior and posterior cardinals. Ligament in a short, posteriorly directed resilifer just within shell margin. Pallial line entire.

Ensitellops hertleini Emerson & Puffer, 1957

(Figures 24–27, 41)

Ensitellops hertleini Emerson & Puffer, 1957:21–22, fig. 2; Keen, 1958:106, 107, fig. 221; Olsson, 1961:242, 509, pl. 36, fig. 9; Keen, 1971:145, 146, fig. 344; Bernard, 1983:33.

Ensitellops pacifica Olsson, 1961:241–242, 553, pl. 80, fig. 9, 9a; Keen, 1971:145, 146, fig. 345; Bernard, 1983:33.

Type material and localities: *E. hertleini*—UCMP 11243, holotype, left valve; length, 8.5 mm (not 9.5 mm, as originally stated); height, 3.2 mm; thickness, 1.1 mm (Figure 24); UCMP 11325, paratype, right valve, length, 6.2 mm; UCMP 11326, paratype, right valve, length, 4.0 mm. UC Loc. A-3603; Guaymas Harbor, Sonora, Mexico (27.9°N); 4 m; *E. pacifica*—ANSP 218893, holotype, left valve (not right, as stated in text; posterodorsal margin now chipped); length, 5.4 mm; height, 2.8 mm; thickness, 0.6 mm (Figure 25); ANSP 218894, paratype, left valve; length, 4.7 mm; UMML 30.9906, two right valves and four left valves, from type locality, labeled “para” [types] by Olsson. El Lagartillo, Las Tablas, Panama (7.8°N); (in fig. caption in error as “Ecuador”).

Description: Shell elongate, cylindrical, length/height about 2.5; beaks approximately 80% of distance to anterior end; overall outline somewhat variable, irregular; typically with a broad, obscure furrow from beaks to central slope, which narrows the anterior end; anterior end

rounded; posterior end slightly pointed to rounded; degree of valve inflation variable, with some specimens fairly flattened, others more inflated, the two valves varying in degree of inflation with no discernable bias as to which valve is more so. Surface with irregular commarginal growth checks and scattered pustules of variable size. Right valve with an anteriorly curved, slightly projecting cardinal; left valve with a vertical cardinal beneath beaks and an anterior cardinal formed by valve margin. Ligament in an elongate, narrow resilifer within valve margin. Left valve with an escutcheon; escutcheon not apparent in right valve. Pallial line broad, evenly curved. Posterior margin of anterior adductor with a raised ridge. Length to 9.4 mm (LACM 40–43.1; Bahía San Felipe, Baja California [Notre]). Additional specimens are illustrated here (Figure 26, 27, 41).

Distribution: From Bahía Cholla, at the head of the Golfo de California (31.4°N) (SMBNH 143664; Skoglund Coll.), south to La Paz, Baja California Sur (24.2°S) (USNM 554978), and Mazatlán, Sinaloa, Mexico (23.2°N) (USNM 565846, 556376); El Lagartillo, Las Tablas, Panama (7.8°N) (type loc. of *E. pacifica*); Santa Elena, Guayas Province, Ecuador (2.2°S) (Olsson, 1961; specimens not located). Other than beach drift, specimens have been obtained from 2 to 35 m (mean, 12 m). Mud and sand bottoms are noted on some labels. I have seen 32 Recent lots.

Discussion: Other than size, there seems to be no basis for separating two eastern Pacific species. As yet, this species is known from only two lots obtained south of Mazatlán, Sinaloa, Mexico.

This species differs significantly from the Pliocene to Recent western Atlantic type species of the genus, *E. protexta* (Conrad, 1841), which is flatter, with a more even outline; *E. hertleini* is more inflated and has a narrower, more produced anterior end. The hinge margin is narrower in *E. protexta*. In the right valve, *E. hertleini* has a more anterodorsally elongate cardinal, whereas in *E. protexta* it is more vertical. In the left valve, the posterior cardinal of *E. hertleini* is heavier and more ventrally directed, and the anterior cardinal is on the hinge margin and is anteroventrally directed. In the left valve of *E. protexta*, the posterior cardinal is slightly posteriorly directed, and the anterior cardinal is more ventrally directed. *Ensitellops protexta* has only a slight escutcheon in the left valve, whereas it is more strongly defined in *E. hertleini*.

Ensitellops hertleini has been confused in collections with specimens of *Sphenia*. *Sphenia* is more inflated, and it has only a small cardinal tooth in the right valve; its right has a resilifer under the beaks, and the left valve has a projecting resilifer. *Ensitellops* is still more likely to be confused with small, elongate specimens of *Hiatella*. Small *Hiatella* have a thicker shell, with conspicuous commarginal folds, a more pointed anterior end, and they

often have two external radial rows of spines. The pallial line, if visible, may be seen to consist of a discontinuous series of irregular scars in *Hiatella*, whereas it is continuous in *Ensitellops*. The hinge of *Hiatella* is heavier at an equivalent size, the protoconch is larger, and there is a heavy nymph for the external ligament.

Fabella Conrad, 1863

Fabella Conrad, 1863:574, 586. Type species (monotypy): *Amphidesma constricta* Conrad, 1841:347, pl. 2, fig. 15. Pliocene, North Carolina. (Concerning this species: Campbell, 1993:32, pl. 10, fig. 94.).

Description: Shell ovate, longer anteriorly. External surface with only commarginal growth checks. Right valve with anterior and central cardinal teeth; left valve with a large anterior cardinal and a small to minute central cardinal. External portion of ligament of moderate length; nymph stout; internal portion of ligament on medial surface of nymph. Pallial line entire.

The following Panamic species was initially placed in *Sportella* Deshayes, 1858:593–595 (type species [original designation]: *Psammotea dubia* Deshayes, 1824 (pp. 76, 6, pl. 10, figs. 13, 14); Middle Eocene, France). *Sportella dubia* differs from taxa here placed in *Fabella* in being equilateral, and it has a longer external ligament and a larger, triangular resilifer.

Fabella stearnsii (Dall, 1899)

(Figures 28, 29, 42)

Sportella stearnsii Dall, 1899:879, 885, 896, pl. 87, figs. 9, 12; Hertlein & Strong, 1947:137–138; Keen, 1958:108, 109, fig. 237; Keen, 1971:143, 145, fig. 341; Bernard, 1983:32 (as *Neaeromya*); Rosewater, 1984:84 (as *Pseudopythina*).

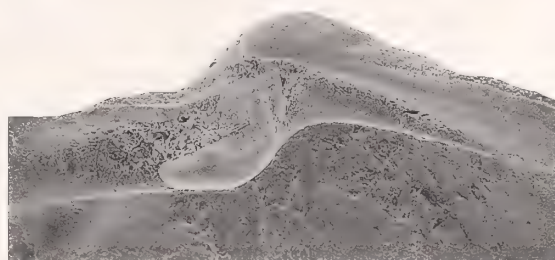
Sportella duhemi Jordan, 1936:146–147, pl. 17, figs. 1, 2.

Type material and localities: *S. stearnsii*—USNM 73701, holotype, pair; length, 13.6 mm; height, 10.0 mm; thickness, 5.1 mm (Figures 28, 42). Golfo de California; no other information available; *S. duhemi*—CASGTC 754.04 (originally 5578), holotype, left valve (not right as stated by Jordan); length, 7.5 mm; height, 4.5 mm; thickness, 1.7 mm (Figure 29). CAS Loc. 754, north of village, Bahía Magdalena, Baja California Sur (24.6°N, 112.2°W); Pleistocene.

Description: Shell ovate; length/height about 0.7; anterior end much longer, broadly rounded; beaks at approximately 40% of distance from posterior end; posterior end subtruncate. External surface with irregular commarginal growth striae. Right valve with a moderate-sized anterior cardinal and a larger central cardinal. Left valve with a large, oblique anterior cardinal, which fits between cardinals of right valve, and a very small central cardinal. Escutcheon absent. External portion of ligament of moderate length, on a stout nymph; internal portion of liga-



27a



27b



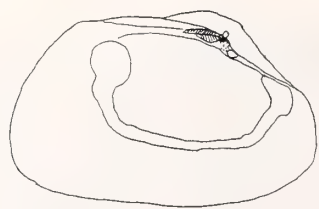
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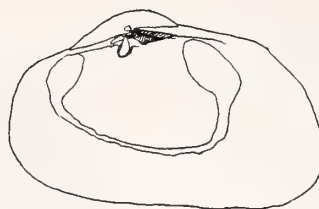
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Explanation of Figures 27–29

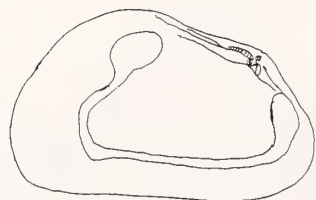
Figure 27. *Ensitellops hertleini*. (a) Left and (b) right valves, close-up of hinges; SBMNH 13083; Topolobampo, Sinaloa, Mexico; left valve length, 6.9 mm; right valve length, 7.2 mm. Figures 28, 29. *Fabella stearnsii*. Figure 28. Holotype of *Sportella stearnsii*, pair; USNM 73701; length, 13.6 mm. Figure 29. Holotype of *Sportella duhemi*, left valve; CASGTC 754.04; length, 7.5 mm.



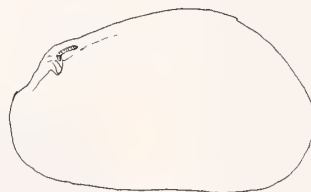
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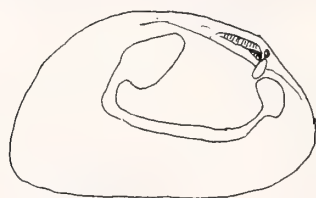
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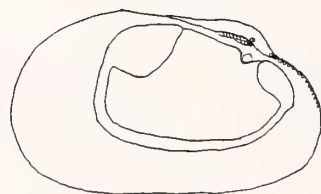
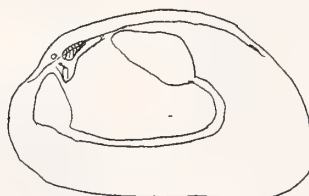
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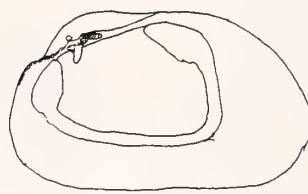
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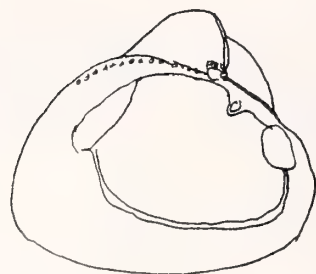
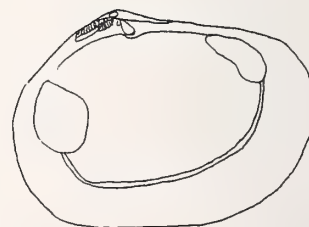
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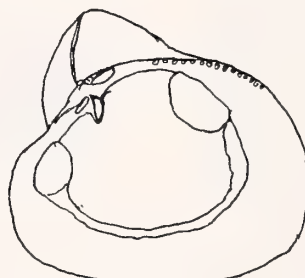
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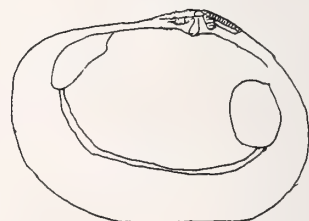
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37



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42



39



40

ment on medial surface of nymph. Pallial line evenly curved. Length to 15.6 mm (CAS 106163; Isla Santa Cruz, Islas Galápagos).

Distribution: Puertecitos, Baja California [Norte] (30.3°N) (SBMNH 144176), south to two stations in the Islas Galápagos: Isla Santa Cruz (0.8°S) (CAS 106163) and Isla Española (1.4°S) (CAS 106387). Records are from 4 to 32 m (mean, 13 m). The only bottom types noted are rock and sand. All the available material was collected dead, except for the holotype, for which no exact locality or habitat was recorded. Known from only 15 Recent lots. Also present in the Pleistocene at Bahía Magellan, Baja California Sur (type locality of *S. duhemi*).

Discussion: Comparing his specimen to Dall's figures of *S. stearnsii*, Jordan (1936) said that *S. duhemi* had a more rectangular shape and more anterior beaks. However, his specimen falls well within the variation of small specimens in Recent lots that are now available. For example, it is closely similar to the specimen in CAS 106386 from Bahía Santa Inez, Baja California Sur, Mexico.

This species differs from the type species of the genus, *Fabella constricta*, in having a shorter posterior end, more oval outline, and a smaller cardinal in the left valve. The external portion of the ligament in *E. stearnsii* is larger, as is the nymph. *Fabella stearnsii* is most similar to the equally rare Recent western Atlantic *F. pilsbryi* (Dall, 1899:884–885, 897, pl. 88, fig. 9), which has a narrower anterior end.

EXCLUDED TAXA

Sportella californica Dall, 1899 (pp. 885, 897, pl. 88, fig. 5), described from Monterey, California, proves to be an *Orobitella* (Galeommatoidea: Lasaeidae) (holotype: USNM 159293) (Coan & Scott, 1997:12, 25).

Anisodonta pellucida Dall, 1916a (p. 30, *nomen nudum*), 1916b (p. 411), also described from Monterey, California, is based on a juvenile mactrid (holotype: USNM

208475), probably *Simomactra falcata* (Gould, 1850: 216).

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Explanation of Figures 30–42

Figures 30, 31. *Basterotia californica*. Figure 30. Left valve; LACM 71–178.50; Punta San Pablo, Baja California Sur; about 26 m; length, 8.9 mm. Figure 31. Right valve; SBMNH 143609; Bahía San Luis Gonzaga, Baja California [Norte]; about 6 m; length, 12.5 mm. Figures 32, 33. *Basterotia obliqua* Coan, sp. nov. Figure 32, holotype, left valve; LACM 2846; length, 9.0 mm. Figure 33, paratype, right valve (pallial sinus not visible); LACM 2847; length, 10.1 mm. Figure 34. *Basterotia panamica*, Coan, sp. nov. holotype, pair; SBMNH 144168; length, 7.3 mm. Figures 35, 36. *Basterotia peninsularis*. Figure 35. Left valve; MNHN; Punta Santa Elena, Guayas Province, Ecuador; length, 18.6 mm. Figure 36. Right valve; CAS 106385; Corinto, Chinandega Province, Nicaragua; length, 13.0 mm. Figures 37, 38. *Basterotia quadrata*. Figure 37. Left valve; LACM 69-24.12; Bahía San Luis Gonzaga, Baja California [Norte], Mexico; 9 m; length 13.0 mm. Figure 38. Right valve; SBMNH 143655; Puerto San Carlos, Sonora, Mexico; 27 m; length, 12.6 mm. Figures 39, 40. *Basterotina rectangularis* Coan, gen. & sp. nov. Figure 39. Paratype, left valve; SBMNH 144175; length 7.8 mm. Figure 40. Holotype, right valve; SBMNH 144174; length 11.0 mm. Figure 41. *Ensitellops hertleini*, right and left valves; LACM 40–43.1; Bahía San Felipe, Baja California [Norte], Mexico; 5 m; right valve length, 5.7 mm; left valve length, 9.4 mm. Figure 42. *Sportella stearnsii*, holotype; USNM 73701; length, 13.6 mm.

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Laboratory Observations of the Feeding Behavior of the Cirrate Octopod, *Grimpoteuthis* sp.: One Use of Cirri

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Abstract. A single specimen from an undescribed species of *Grimpoteuthis* (Octopoda: Cirrata) was examined in captivity for 53 days. It was successfully fed both brine shrimp (*Artemia*) nauplii alone and a mixture of adult brine shrimp with nauplii. Three distinct feeding modes were observed. The first, envelopment, was only exhibited when nauplii alone were presented. The second, entrapment, was exhibited when the mixture of nauplii and adults was presented. The third, cirri-generated current feeding, showed that the cirri in this animal beat in coordinated metachronic patterns to generate currents which transport individual adult brine shrimp under the bell and toward the mouth. Indirect observation suggests these cirral currents function in the other two feeding methods as well.

INTRODUCTION

Techniques for maintenance, rearing, and culture of shallow-water cephalopod species have improved greatly over the past 15 years, (see Boletzky & Hanlon, 1983; Hanlon, 1987; Hanlon, 1990). However, there have been no reports of successful long-term maintenance of cirrate octopuses in aquaria. One notable report on the behavior of the cirrate octopod *Opisthoteuthis* Verrill, 1883, was presented by Pereyra (1965) using specimens housed in shipboard aquaria. Long-term laboratory study has been limited because cirrate octopods are extremely delicate animals which live too deep to be collected by SCUBA divers, while trawl or plankton nets invariably damage them. In order to gather specimens in good condition, a submersible with appropriate collecting chambers must be used.

A single cirrate octopod of the genus *Grimpoteuthis* Robson, 1932, was collected by a submersible and maintained for nearly 2 mo in an aquarium. Three distinct feeding modes were observed, including direct observation that the cirri beat in metachronic activity patterns to assist transport of prey toward the mouth.

METHODS

The Monterey Bay Aquarium Research Institute's (MBARI) research vessel R/V *Point Lobos*, carries a Hysub model ATP 40-1850, a remotely operated vehicle equipped for exploration to depths of 1000 m (see Robison, 1993). A Sony DXC 3000 camera aboard the ROV records images of animals *in situ* on high resolution Betacam videotape. All information, including time-code and scientific observations from the audio track of the videotape, is entered into a computer database.

A 7.5-L canister (Youngbluth, 1984) allows animals to

be collected without being harmed physically. The collector is a clear Plexiglas tube with pivoting top and bottom lids that move laterally in unison to open or close the tube. The ROV pilot maneuvers the open tube over an animal without touching it, and then seals the animal and the water surrounding it inside the cylinder.

On 8 April 1994, a specimen-collecting dive for the Monterey Bay Aquarium caught a single *Grimpoteuthis* specimen at a depth of 284 m. The animal was brought to the surface and was moved within 2 hours to a 15 gallon Plexiglas aquarium (44 cm × 34 cm base; 38 cm height) at MBARI's laboratory in Moss Landing, California. The facility has aquaria in a temperature- and light-controlled laboratory designed for observation of deep-sea specimens. The seawater system is a closed recirculating type with a 350 gallon reserve tank and sand filtration. Water in the reserve tank is changed monthly. Temperature is maintained at a target of 4°C (± 0.5°C) and salinity is maintained at a target of 34 ppt (33.7–34.4 ppt). The temperature and salinity of the water in the laboratory tank were similar to the water from the sampler and so the octopod was dipped directly into the aquarium. The apparent condition of the animal was excellent upon transfer into the tank. It bobbed near the surface for a short time, then settled to the bottom. The animal was left overnight to acclimate to its new surroundings. Observations were made over a period of 53 d. The laboratory was dark except when observations were made with the aid of a red light. Observations also were made using a Litton Model 982 (Gen 2.5 photo-multiplier chip) night-vision monocular with infrared beam. Observations and feeding trials were conducted every third day for a period of 30 min–1 hr. During the first two trials, pieces of fresh fish and other seafood bought at a local fish market were offered without success. For

the third attempt, live *Artemia* nauplii were offered, accepted, and subsequently used throughout the study. The brine shrimp were reared in inverted pyramid-shaped aquaria using 2 tbs. of eggs in 4 L of water. The shape of the aquaria allowed nauplii to concentrate near the bottom tip where 100 mL was siphoned off for food. New cultures were started weekly. Beginning with the fourth attempt, adult brine shrimp supplied by the Monterey Bay Aquarium were also added to the nauplii. The nauplii were added to adults in a 250 mL beaker such that the resulting mix contained about 10 to 20 adults.

RESULTS

During the 53 days in captivity, 14 displays of feeding were observed. After death, the animal, a mature female, weighed 39.3 g and had a total length of 78 mm. The animal was not weighed before this time to avoid disturbing it, but no appreciable difference in size was observed during the period of captivity.

This octopod died after an unusual drop in salinity occurred in the aquarium (to 33.4 ppt), whereupon the specimen was transferred to another aquarium, but by then the fins were small and discolored and the condition of the animal appeared poor. It died the next day, releasing 18 undeveloped eggs through a tear in the mantle wall tissue located behind the siphon. The eggs were immature, lacking the secondary capsule, and did not therefore represent a spawning of the animal. The ovaries were exposed through this tear, and they contained more eggs of varying sizes. Smaller eggs were nearest the mantle apex. Larger eggs were farther inside the mantle, toward the base of the ovary.

General Behavior

The animal was in excellent condition when placed into the aquarium, with only a small wound on the mantle epidermis, which healed during the first several weeks. The fins of cirrates and midwater squids are indicative of general health (personal observation). With rare exception, specimens with frayed, discolored, or otherwise damaged fins soon die. The fins of this specimen looked completely healthy throughout the observation period. When the animal was active, it bobbed continually at the surface. This action eventually stretched the tissue around the area of the posterior mantle which breached the surface, but without ill effect.

When observed using night vision, the octopod spent most of its time resting on the bottom of the tank, occasionally swimming (once or twice per hour) to the surface and then settling back to the bottom. Under dim red light, it became more active, swimming and bobbing near the surface as soon as the light was turned on, eventually settling back down to the bottom. After it settled, it would resume the behavior exhibited when observed using night vision (only swimming once or twice per hour). During

the first two weeks; the active swimming and bobbing period under red light lasted from 8–12 min. By the final 2 weeks, that active time had reduced to 4–6 min, suggesting the animal was becoming accustomed to the disturbances of turning on the red light. When resting on the bottom, the arms were curled forward along the web margin, the tips oriented dorsally (away from the siphon), such that the tips of the first arms nearly touched, and the other three arm pairs oriented similarly along either side.

Locomotion

The principal means of locomotion was the medusoid-like contractions of the bell-shaped concavity created by the arms and interbrachial webbing. Contractions occurred at a rate of about 1.2 per sec. Fins often supported this movement with simultaneous beats, at a rate of 2 to 3 fin strokes for every medusoidlike contraction. A fin stroke almost always occurred at the same time as a contraction. Yet the fins also acted independently—rotating back and forth to control attitude and direction during swimming and when passively sinking to the tank floor.

Feeding Behaviors

The *Grimpoteuthis* exhibited three distinct feeding modes: (1) envelopment, using the arms and web to envelop prey within the oral surface of the web (Figure 1a); (2) entrapment, using the tank bottom to trap prey beneath the bell-shaped expansion of the arms and web (Figure 1b); and (3) cirri-generated current feeding, creating currents using the cirri to draw prey beneath the web margin between two arms of the resting cephalopod (Figure 1c).

1. Envelopment: During the first week, only non-living foods were offered, including pieces of fish, crab, shrimp, squid, and fish roe. However, they did not elicit any feeding behavior. When live *Artemia* nauplii were poured directly over the octopus swimming near the top of the tank, the cirrate immediately opened its arms and web wide and enveloped a dense group of brine shrimp within the arm webbing. The octopod sank to the bottom of the tank and the inflated arm-web remained pinched shut, but the enclosed volume proceeded to shrink in size, first distally, working the shrimp toward the beak. This entire behavioral sequence was repeated once more during this feeding session.

Cirri occur along the oral surface of the arms and are arranged in two rows. The distal edge of the interbrachial web (the web margin) is what pinches closed, enveloping concentrations of planktonic prey. The volume of water is reduced by gradual contraction of the brachial web and arms, progressing from the arm tips toward the mouth. The result is a continually reducing volume of water with an increasing prey density near the mouth. As water slowly escapes through the small aperture created by the arm

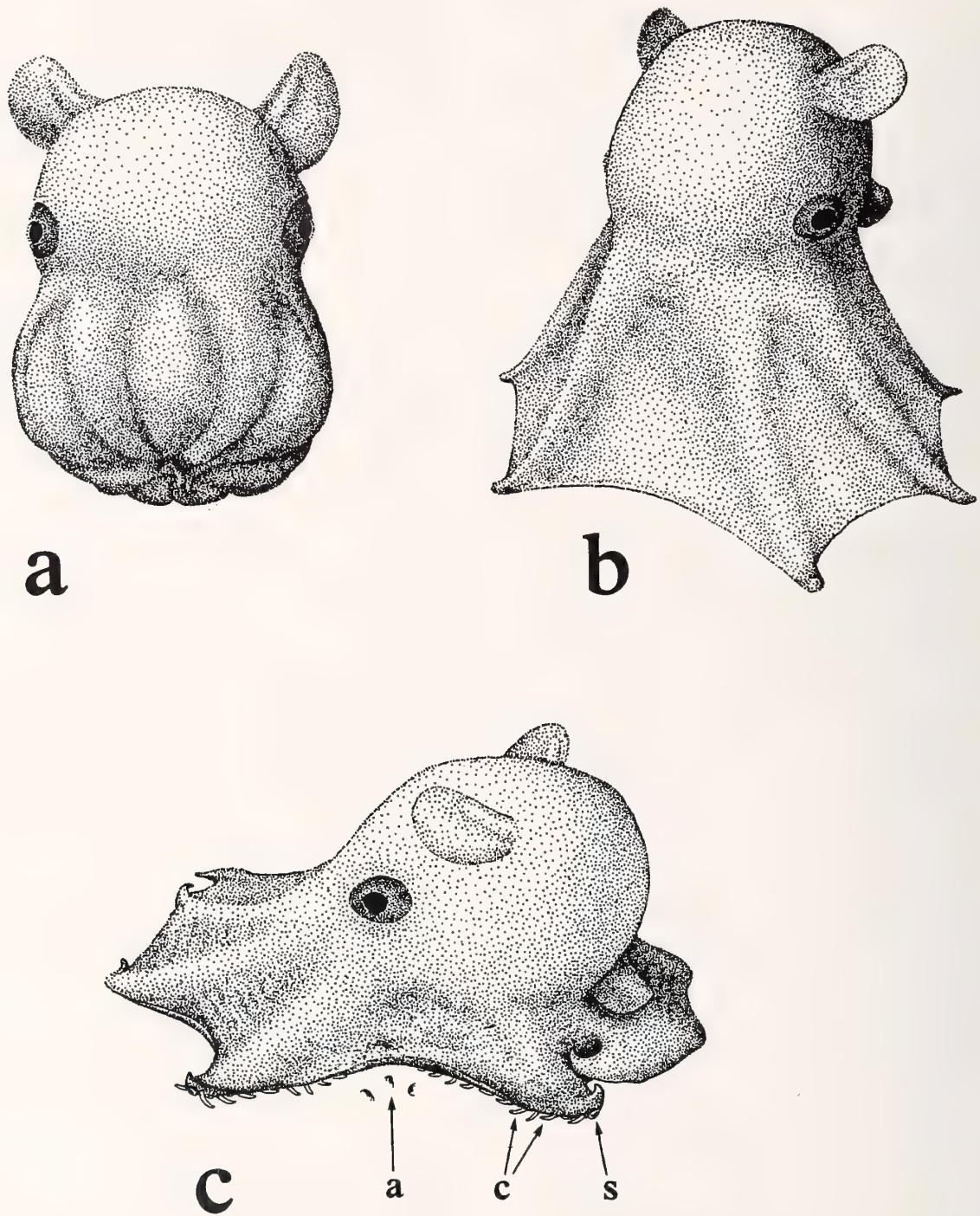


Figure 1

(a) The envelopment feeding behavior of *Grimpoteuthis*. (b) The entrapment feeding behavior of *Grimpoteuthis*. (c) The cirri-generated current feeding behavior of *Grimpoteuthis*. a, Artemia; c, cirri; s, sucker.

tips, it appears there is some mechanism preventing the prey from escaping with the water. Though direct observations were not possible, it appears that the cirri aid in pushing prey toward the mouth. Rippling patterns on the arm-web tissue were highly suggestive of cirri movement underneath that would be similar to the observable cirri activity described below in the cirri-generated current feeding behavior.

2. Entrapment: In order to increase the amount of food ingested, adult *Artemia* were added to the beaker of nauplii during the next feeding sequence, with similar envelopment followed by trapping of food against the bottom. After enveloping and eating the shrimp, the *Grimpoteuthis* swam to the top of the tank, extended its arms such that the webbing became bell-shaped, and sank through the water to the tank floor (see photo in Pereyra (1965, fig. 3e)). The animal controlled its attitude, keeping the tips of its extended arms directed downward, by making small adjustments using its fins, but the fins did not actively push the animal down—it sank due to its slightly negative buoyancy. During its descent, it trapped shrimp beneath the rim of the bell-shaped arm-web. When the octopod settled, it forced prey into its mouth by forcing the water beneath the oral surface toward the mouth. To accomplish this, the points located about one-fourth of the arm length from the tip of each arm were pulled together creating an enclosed volume of water. The tips of the arms remained on the bottom; the arms curled inwardly to meet and isolate a volume of water. As the arms contracted slowly beginning where the inner surfaces of the arms touched, the enclosed volume became progressively smaller. When the volume was confined to the area created within the proximalmost one-third of the arm-web, it stopped reducing further. The animal held this position for several minutes, after which it opened its arms and began moving. Only a few shrimp were seen escaping from the region under the arm-web. It is clear that the vast majority of the prey in the swarm trapped along the bottom were eaten. Once again, I believe the cirri assisted food transport due to the ripples seen in the arm-web, but I have no direct evidence of cirri movement for this feeding behavior.

3. Cirri-generated current feeding: Entrapment against the bottom was exhibited for the remaining weeks, with envelopment observed only once more. Trapping usually was displayed twice at each feeding, followed by cirri displacement feeding behavior where the octopod remained on the bottom and drew individual adult brine shrimp into a gap created by lifting one section of its web margin between two adjacent arms and subsequently creating slow currents of water using the cirri. When a portion of the margin was lifted high enough, cirri were observed aligned toward the edge and moving in metachronic waves toward the mouth. Furthermore, individual shrimp were observed being pulled into the opening by

these waves, often against the direction they were swimming.

The cirri were clearly observed beating in coordinated metachronic waves to create currents to draw food into the concavity of the oral surface of the arm-web. Currents were generated by the cirri along two adjacent arms in opposite directions such that individual brine shrimp were drawn to the edge of the webbing between these two arms. The beating action of each cirrus includes a quick contraction of muscles along one side, bending the structure into an arc. The cirrus recoils and regains its original shape relatively slowly compared to the contraction, but it is ready to beat again in time for the next wave. I estimated the periodicity of these waves to be 1 per sec, and that the cirrus recoil takes about twice as long as the contraction.

DISCUSSION

The adaptive significance of the cirri that characterize cirrate octopods has received little attention in the literature. Young (1977) noted that cirri have large nerves and serve a sensory role, probably to detect the presence of food. Villanueva & Guerra (1991) suggested that microvilli and fusiform structures, detailed using SEM, may serve an "olfactory-like" role similar to the role suggested for the cirri of *Vampyroteuthis* Chun, 1903. It is clear from the current study that at least one functional role of the cirri for this *Grimpoteuthis* species is to assist in food capture and transport. I note here that the cirri of *Vampyroteuthis* do not appear to be used in the manner described in this paper and thus may provide a different role for vampyromorphs (Hunt, personal observation).

Many of the moving and resting behaviors described here concur with those given for *Opisthoteuthis* by Pereyra (1965). Specifically, the resting position, swimming, and bobbing behavior, and function of fins in balancing and attitude adjustment are virtually identical in all respects between the specimens from both studies.

Some of the behaviors witnessed here had been suspected from the morphology of cirrates. Pereyra (1965) speculated that such trapping may be possible although he had no direct evidence. Berry (1952) speculated that cirri may be used to move micro-plankton toward the mouth, but he gave no clear explanation as to how this would be accomplished.

Gut-content analysis on one individual indicates that this species feeds on swarming micro-polychaetes (Hochberg, personal communication). The stomach contents discussed for three *Opisthoteuthis* species show that these animals feed on tiny prey, predominantly crustaceans and polychaetes (Pereyra, 1965; Villanueva & Guerra, 1991). Pereyra (1965) noted that very little sediment appeared in the stomach of *Opisthoteuthis*. Yet this *Grimpoteuthis* sp. has been observed to feed by sitting on the bottom and stirring up sediments to flush out infaunal microorgan-

isms (Hochberg, personal communication). It is difficult to determine whether these observations reflect a behavioral difference between genera or whether a suite of feeding behaviors is used by various cirrates under different circumstances. The issue is further confused because the traits used for classifying these genera are still being debated (Hochberg, personal communication).

Nevertheless, for such tiny prey to be ingested in useful numbers, they must be captured in groups. An animal living along the bottom may be able to trap prey using the surface. But there is nothing against which to trap prey in the open space of the water column. Given that *Grimpoteuthis* has been observed in the water column 50 m above the bottom and reacted immediately to envelop a group of swarming shrimp nauplii, it is likely that the envelopment mode could be used to capture food above the sea bed. Entrapment or cirri-generated current feeding would be useful only along the bottom. Thus it seems reasonable to postulate that the behaviors exhibited in aquaria have natural correlates.

It is of course possible that the changing modes of feeding exhibited in this study reflect confinement in a small aquarium. However, one fact suggests the behaviors observed resulted from the food presented and not the tank itself. Food was always introduced in the same manner, poured directly over the head of the octopod as it swam near the surface. In the third trial when only *Artemia* nauplii were presented in a dense cloud directly around the octopod, envelopment was observed. Yet on subsequent trials when adult brine shrimp were added to the swarm of nauplii, envelopment was quickly abandoned for entrapment. During these feeding bouts, entrapment occurred first (usually twice), followed by cirri-generated current feeding, the latter being used primarily to capture adult brine shrimp. Future experiments introducing a varied feeding regime of brine shrimp adults and/or nauplii should demonstrate clearly whether these feeding behaviors are indeed reflective of a natural response to various food sizes and concentrations, or an artifact of captivity.

Incirrate octopuses have a reputation for being easy to care for in laboratory aquaria. Relatively shallow-water cirrates, such as *Grimpoteuthis* or *Opisthoteuthis* may

also be good aquarium animals, though they would be somewhat more difficult to maintain than incirrates, as special attention needs to be given to light, temperature, and oxygen conditions.

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Ontogenetic Changes in Boring Behavior by the Rock-Boring Bivalve, *Barnea manilensis* (Pholadidae)

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Abstract. Ontogenetic changes in morphology related to boring behavior by *Barnea manilensis* (Philippi, 1847) were observed. The shell outline changes from round to elongate during the transition from pediveliger to juvenile stages. Along with such a morphological change, the boring style gradually changes from anterior boring in early round-shelled juveniles, where the opening of the anterior valve margin, with rotation around a dorso-ventral axis, abrades the burrow wall, to ventral boring in older and larger long-shelled individuals, which open the ventral margin with rotation around a longitudinal axis (hinge line) for abrasion. This observation, with an examination of the literature, leads to the suggestion that early juveniles of all pholads employ anterior boring. Later, many pholads continue anterior boring throughout life, whereas others gradually shift toward ventral boring. In addition, anterior boring is thought to be a primary character of pholads, and ventral boring a specialized character derived from anterior boring.

INTRODUCTION

Barnea manilensis (Philippi, 1847) is a common bivalve of the Pholadacea which bores into soft rock (e.g., mudstone and shale) of the intertidal zone and, in Japan, occurs from Hokkaido to Okinawa (Habe, 1977). Boring behavior occurs not only in the Pholadacea, but also in the Myacea, Mytilacea, Veneracea, Cardiacea, Gastrochaenacea, and Hiatellacea (Yonge, 1963; Ansell & Nair, 1969). Among these superfamilies, species of Pholadacea are characterized by an ability to bore into a variety of substrata, such as mud, rock, and wood. Accordingly, the Pholadacea exhibit considerable modifications to shell form as a reflection of its varied boring habits (Nair & Ansell, 1968; Röder, 1977; Seilacher, 1985). The Pholadidae, including *B. manilensis*, bore into mud, rock, and other solid substrata and are regarded as less specialized for boring than the wood-boring Teredinidae (also Pholadacea) (Nair & Ansell, 1968).

The boring mechanism of the Pholadacea has been studied extensively (Miller, 1924; Nair & Ansell, 1968; Röder, 1977; Seilacher, 1985). Pholads are generally considered to be mechanical borers (Miller, 1924; Yonge, 1963; Ansell & Nair, 1969), although chemical boring has also been suggested (Smith, 1969; Morton, 1985, 1986). The boring procedures of pholads have been detailed for the wood borer *Teredo* (Teredinidae) (Miller, 1924), the rock borer *Zirfaea crispata* (Pholadidae) (Nair & Ansell, 1968), and the mud borers *Cyrtopleura costata* and *Barnea candida* (Pholadidae) (Röder, 1977; Seilacher, 1985). The boring behavior of wood borers in their early ontogenetic stage has been outlined with special emphasis on behavior and morphology (Isham & Tierney, 1953; Turner & Johnson, 1971). Ontogenetic changes in morphology

related to boring behavior in rock-boring pholads have not, however, been well documented.

In the present study, ontogenetic changes in shell and tissue morphologies were observed for *B. manilensis*. Along with these morphological changes, *B. manilensis* undergoes a conspicuous change in boring style. It changes from anterior boring, where the opening of the anterior valve margin with rotation around a dorso-ventral axis abrades the burrow wall, to ventral boring, or opening the ventral margin with rotation around a longitudinal axis (hinge line). The present study describes this change in boring style. Based on comparison with other boring pholads, the significance of this ontogenetic change in *B. manilensis* is discussed in relation to specializations in boring style by pholads.

MATERIALS AND METHODS

Living specimens of *Barnea manilensis* were collected from within tuffaceous mudstone at Itsuwa-machi, Kumamoto, western Japan, in September 1994. Larger individuals were kept alive in seawater tanks at the Aitsu Marine Biological Station of Kumamoto University. Individuals were extracted from the rock without destruction of their shells for later observation of morphology and boring behavior. Their gametes were also obtained from the gonads by dissection and were fertilized in experimental dishes. By culturing their larvae, numerous individuals were obtained for observation of their pediveliger larval and post-larval development. Larvae were cultured in seawater (salinity = 31–34‰; temperature = 21–25°C). When the larvae formed a foot and entered the pediveliger stage, fragments of the mudstone in which the adult parents had lived were placed in the culture con-

ainers as a substratum for their settlement and boring. Crawling and boring behavior were observed with a binocular microscope for more than 50 individuals of pediveliger larvae and post-larvae, and recorded with a video camera.

More than 50 specimens of pediveliger larvae and post-larvae were fixed in a solution of commercial sugar (10%), formalin (1%), and sodium bicarbonate (0.05%) in seawater (Castro & Le Pennec, 1988) in order to observe the hinge and muscle structures with an optical microscope (Sakai & Sekiguchi, 1990). Further, after fixing, the shells were cleaned and separated using sodium hypochlorite, in order to observe the form and structure of the shells with a scanning electron microscope (SEM).

Specimens of the post-larval boring stage of *B. manilensis* were also collected for morphological observations from intertidal mudstones at Cape Taito, Chiba, Japan, in June 1991. In order to examine shell development, 30 specimens of pediveliger larvae reared in a culture tank, and 90 specimens of boring-stage shells collected from Cape Taito, were measured. Shell size was measured from SEM photographs, optical photographs, and sketches.

All specimens examined are deposited in the University Museum, University of Tokyo (UMUT).

OBSERVATIONS

Ontogenetic Changes in Shell Morphology

Besides the clearly apparent change of its shell outline from round to elongate, *Barnea manilensis* exhibits other ontogenetic changes in shell and soft body morphologies during the transition from pediveliger to juvenile stages. Because these changes are intimately related to the change in its boring behavior, they will be described in detail below.

Ontogenetic changes in shell and tissue morphologies may be divided into four stages, termed A, B, C, and D. Stage A corresponds to the pediveliger stage. The beginning of stage B is defined by the addition of a dissoconch with formation of the ventral condyle and umbonal reflection. The extension of the reflection toward the posterior over the dorsal condyle (umbo) in turn defines the beginning of stage C. Stage D is defined by the disappearance of the ventral condyle. The morphological terms used here are given in Figure 1.

Stage A: The round shell with a long provinculum in the pediveliger stage has concentric growth lines and a nearly smooth ventral valve margin, but lacks a ventral condyle ($L = 0.23\text{--}0.30$ mm) (Figures 1A, 2A). Each of the two adductor muscles extends perpendicular to the sagittal plane of the shell (Figure 3A) and their thickness does not vary throughout their length.

Stage B: This stage represents a short period during and following metamorphosis ($L = \text{approx. } 0.3\text{--}0.8$ mm) (Figures 1B, 2B). The ventral valve margin protrudes

ventrally to form a thick and solid ventral condyle: the left condyle has a notch to accommodate the knobby tip of the right condyle. The ventral condyle leaves its trace as an umbonal-ventral sulcus externally and as a ridge internally as the shell grows. The umbonal-ventral sulcus divides the dissoconch into anterior and posterior parts. The anterior external surface has conspicuous growth lines and radial ribs which form undulating denticulate ridges (Turner, 1969) at their intersections. The posterior surface is less ornamented than the anterior and has weak concentric growth lines.

The protruding ventral condyles produce two gapes along the ventral valve margin when the valves are closed: the anterior pedal gape and the posterior siphonal gape. The siphonal gape is narrow immediately after metamorphosis begins, then widens as the posterior margins become more concave with growth.

The two valves make contact at the dorsal condyles (Figure 3B) and are connected by a ligament, located just posterior to the dorsal condyles, and extending between the recessed resilifer of the right valve and the dorsal surface of the chondrophore on the left valve. The ligament and the left chondrophore are fully developed in a newly metamorphosed individual, but they become reduced rapidly toward the end of this stage.

The anterior adductor muscle (**AAM**) is symmetrical between the two valves, and attaches anterior to the dorsal condyle (umbo). It extends toward the umbo with development of the outward reflection of the antero-dorsal margin. This reflection is termed the umbonal reflection (Turner, 1969). The posterior adductor muscle (**PAM**) extends obliquely to the shell's sagittal plane during this stage (Figure 4B). Its right end attaches to the inner surface of the right valve, whereas its left end is located more posteriorly on the slightly outwardly bent and thickened postero-dorsal margin of the left valve. The **PAM** becomes thicker from left to right, and its scar on the right valve is about two to four times as large as on the left.

Stage C: This stage is transitional between stages B and D ($L = 0.8\text{--}2.0$ mm) (Figures 1C, 2C). The shell is longitudinally elongate and oval in shape, but the ventral condyle is still present. Denticulate ridges cover the anterior external valve surface in the early part of this stage, as they do in stage B. By the end of this stage, these denticulate ridges also appear on the posterior surface, although they are less conspicuous than the anterior ridges. The siphonal gape of the posterior valve margin widens. The pedal gape narrows but becomes longitudinally extended. The ligament and chondrophore become vestigial (Figure 3C).

The posterior part of the umbonal reflection, where the **AAM** attaches, extends posteriorly beyond the dorsal condyle. This part of the **AAM** is called the **AAM-P** herein, and the anterior part of the **AAM** is termed the

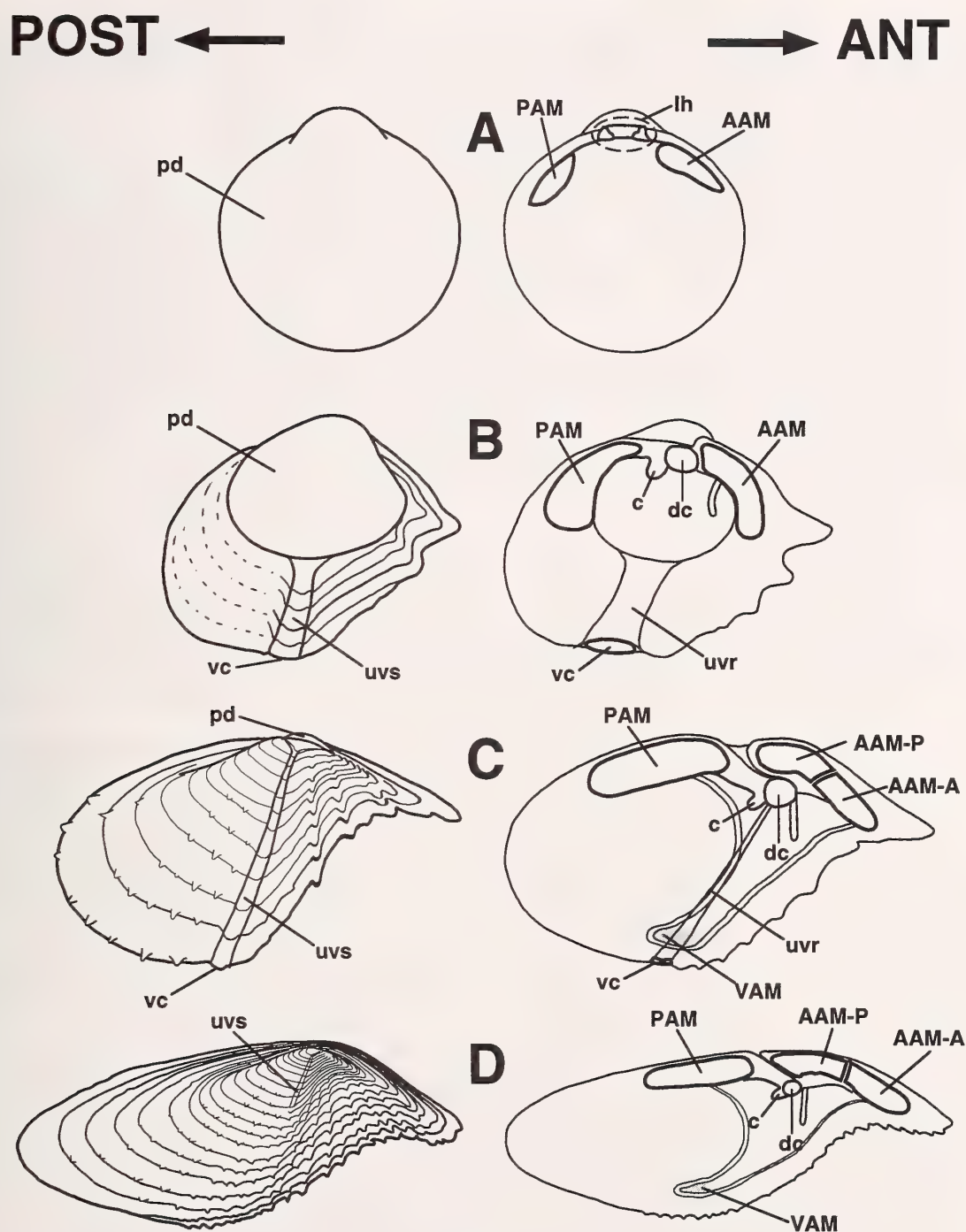
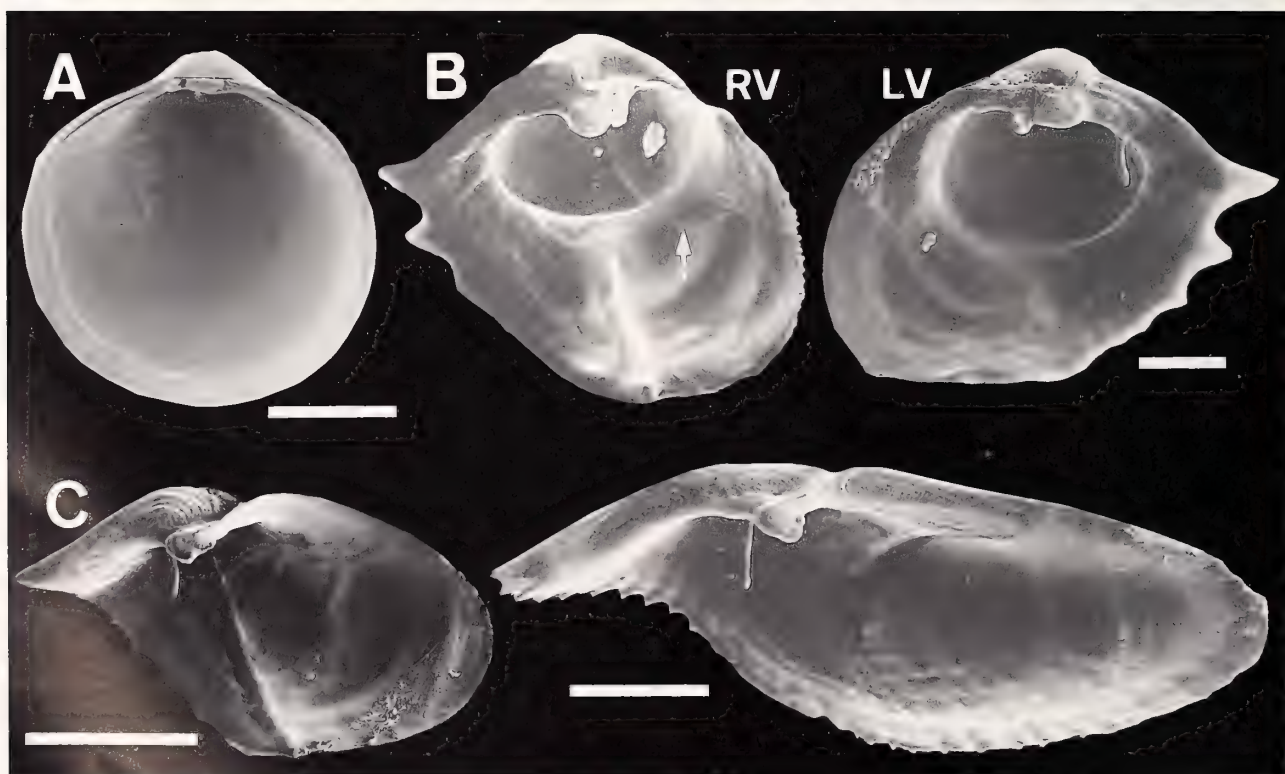
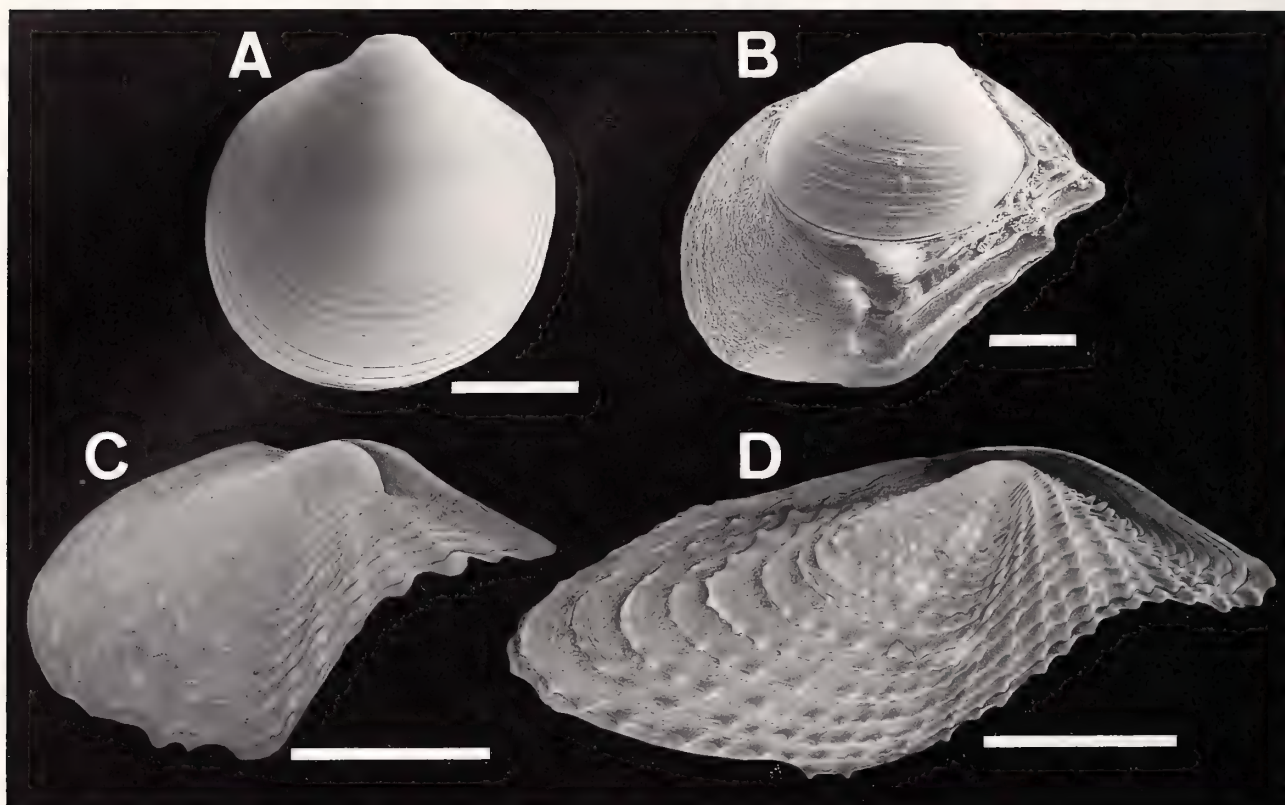


Figure 1

Morphological characters of four stages of *Barnea manilensis*. External views of right valves (left side). Internal views of left valves (right side). **ANT** = anterior; **POST** = posterior. **AAM** = anterior adductor muscle scar; **PAM** = posterior adductor muscle scar; **VAM** = accessory ventral adductor muscle scar; **c** = chondrophore; **dc** = dorsal condyle; **lh** = larval hinge; **pd** = prodissococonch (larval shell); **uvr** = umbonal-ventral ridge; **uvs** = umbonal-ventral sulcus; **vc** = ventral condyle.



AAM-A. The **PAM** becomes almost equal in diameter at its right and left ends, and again becomes nearly symmetrical with respect to the sagittal plane. The accessory ventral adductor muscle (**VAM**) scar becomes apparent in this stage. The **VAM** attaches to the posterior angle of the pallial line on the umbonal-ventral ridge of each valve. The right and left mantle margins are fused around the **VAM**.

Stage D: This stage is defined by the disappearance of the ventral condyle and is usually represented by larger individuals ($L > \text{approx. } 2.0 \text{ mm}$) (Figures 1D, 2D). The shell is slender. The umbonal-ventral sulcus is reduced to being merely one of the radial furrows, so that division of anterior and posterior valve surfaces becomes obscure. Denticulate ridges appear on the whole external surface, although more conspicuously anteriorly. Although the ventral condyle disappears, the pedal and siphonal gapes remain.

The ligament disappears at this stage. The chondrophore is reduced to a tiny spine, which protrudes from the dorsal condyle (Figure 3D).

The **AAM** attachment area becomes larger than that of the **PAM** in this stage, and the **PAM** becomes symmetrical. The **VAM** attaches to a prolongation of the line of the umbonal-ventral ridge (which disappears in this stage).

Allometric Shell Growth

The round larval shell (stage A) of *Barnea manilensis* becomes more elongate in larger individuals (stage D). The L/H ratios of pediveliger larval shells (stage A) are about 1.0. These ratios rapidly increase through stages B, C, and the earlier part of stage D ($L = \text{approx. } 7\text{--}10 \text{ mm}$) (Figure 5a), then stay almost constant afterward ($L/H = \text{approx. } 2.7$) (Figure 5b).

The dorso-ventral axis passes through the dorsal condyle (umbo) and the ventral condyle (or **VAM** scar). As the axis changes from acline in stage B to prosocline in stage D, the angles (**DVA**) between the longitudinal axis (or hinge line) and the dorso-ventral axis rapidly decrease from about 80 degrees in stage B to about 40 degrees in stage D at about 10 mm in shell length, and then stay almost constant for the remainder of life (Figure 5c). The **DVA** and the shell shape (L/H) show a positive correla-

tion ($r = 0.94$), which means that a more slender shell has a more prosocline dorso-ventral axis (Figure 5d).

Crawling and Boring Behavior of *Barnea manilensis*

The pediveliger of *Barnea manilensis* (in growth stage A) does not bore but crawls with a simple set of movements (Figure 6A). It extends its foot anteriorly, opens the valves ventrally and attaches the tip of its foot to the substratum. It then closes its valves, its foot contracts, and the resulting motion pulls the body forward. It then relaxes the muscles and the valves gape ventrally. The valve opening in this crawling sequence is only the inevitable result of extrusion of the foot.

It should be mentioned that when growth stage B is reached and boring begins, boring ability is acquired by adding another step to the crawling sequence (Figure 6B), when it opens the anterior margin of the valve. This newly added step follows pulling of the body forward by contraction of the foot, in which anterior parts of the closed valves are pressed against the substratum (burrow wall). When the anterior valve margin opens, the anterior valve surfaces abrade the burrow wall (Figure 7B). This is required for boring. The process of boring in stage B is here called anterior boring. This movement is derived from a new muscular movement, which takes place by contracting the **PAM** and relaxing the **AAM** (Figure 8B). These muscles work reciprocally to accomplish anterior boring.

The boring movement changes with growth, from anterior boring in stage B to ventral in stage D (Figure 7). An individual in stage B opens only its anterior valve margin (Figure 7B) but, with growth, it tends to open its valves more ventrally. By stage D, ventral valve margin is opened to abrade with both valves' entire surfaces (Figure 7D). This is called ventral boring. An individual in stage C is transitional between stages B and D, opening its antero-ventral valve margin (antero-ventral boring) (Figure 7C).

Development of Boring Behavior

Stage A: Boring movement does not occur in this stage, although vigorous crawling activities do. No morphological specialization for boring is observed at this

Figure 2

Scanning electron micrographs of four stages of *Barnea manilensis* shells. External views of right valves (upper figure) (A. UMUT RM 27598; B. UMUT RM 27599; C–D. UMUT RM 27597). Internal views of right valves and two valves (lower figure) (A. UMUT RM 27600; B. UMUT RM 27601; C–D. UMUT RM 27596). LV = left valve; RV = right valve. arrow = margin of right **PAM** scar in stage B. Scale bar: A = 100 μm , B = 100 μm , C = 500 μm , D = 1 mm.

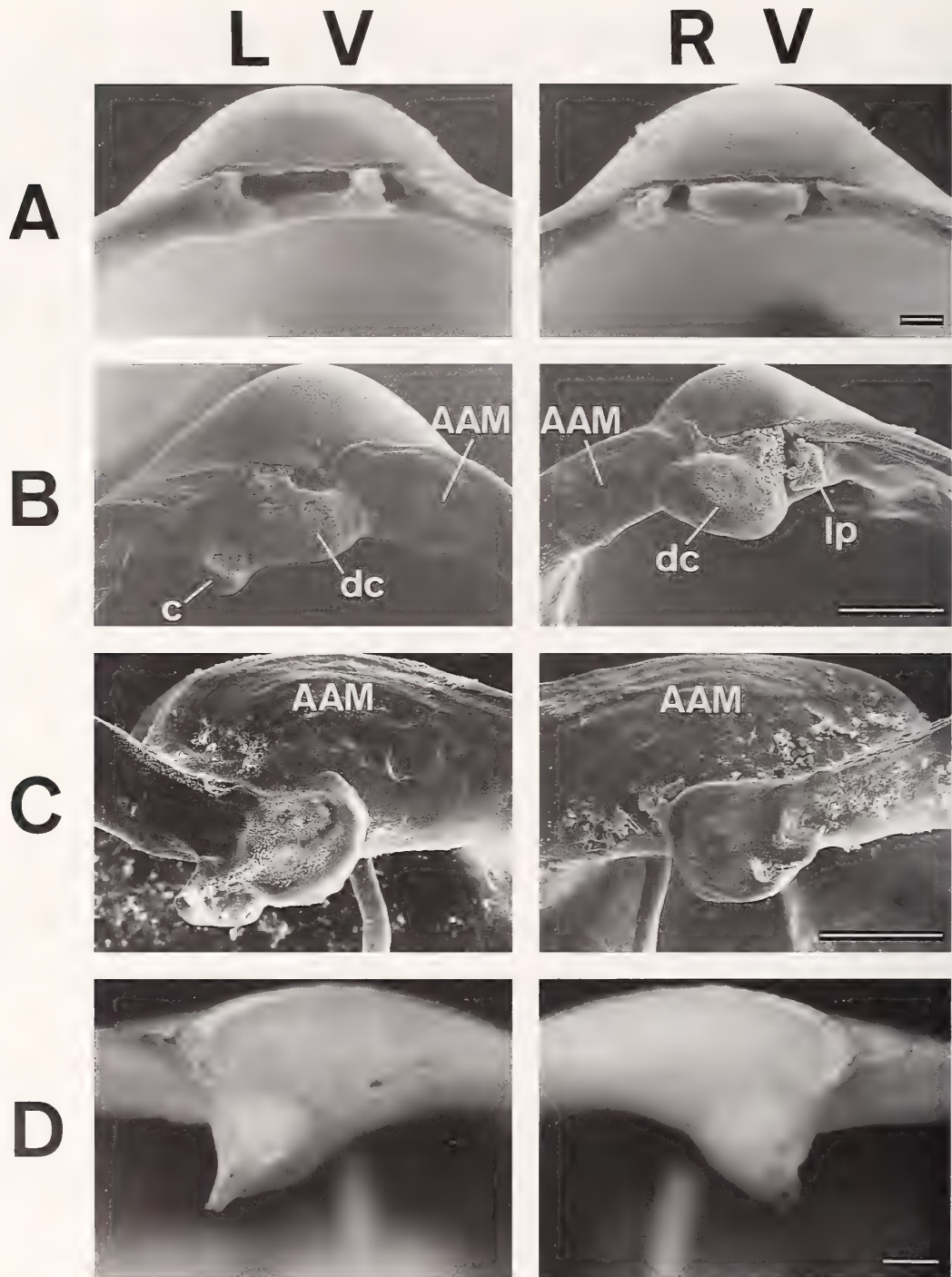


Figure 3

Photographs of the hinge regions of four stages of *Barnea manilensis* (A. UMUT RM 27600; B. UMUT RM 27602; C. UMUT RM 27596; D. UMUT RM 27594). A–C = Scanning electron micrographs. D = Photographs (shell length = 33 mm). LV = left valve; RV = right valve. c = chondrophore; lp = ligament pit; dc = dorsal condyle; AAM = anterior adductor muscle scar. Scale bar: A = 10 μ m, B = 50 μ m, C = 100 μ m, D = 1 mm.

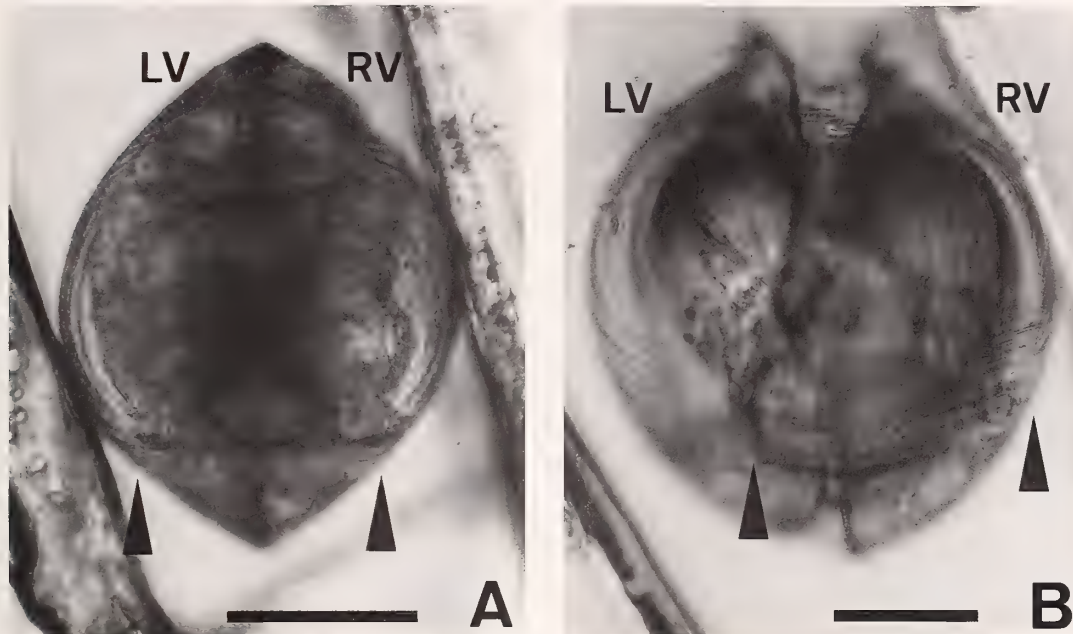


Figure 4

Photomicrographs showing dorsal views of articulated valves of *Barnea manilensis* in stage A (left) and stage B (right). In stage A (pediveliger larva), the **PAM** extends perpendicular to the sagittal plane of the shell. In stage B (metamorphosing individual), the **PAM** extends obliquely to the sagittal plane. LV = left valve; RV = right valve; arrows indicate attachment positions of the **PAM**. Scale bar = 100 μ m.

stage. The hinge and musculature enable the valves to rotate around the longitudinal axis (= hinge line), as do the majority of larval bivalves (Figure 7A). The two adductor muscles of the larva are employed only for closing the valves. The relaxation of both adductor muscles leads to a gape along the whole ventral margin.

Stage B: The anterior external surfaces of the valves abrade the burrow wall (anterior boring), when the anterior valve margin opens widely to rotate around the dorso-ventral axis by contraction of the **PAM** (Figure 7B). When the **PAM** contracts, the **AAM** is stretched (Figure 8B). This reciprocal movement of the **PAM** and **AAM** has also been described for *Teredo navalis* (Miller, 1924) and *Jouannetia cumingii* (Morton, 1986). The thick and solid ventral condyles fit tightly together by the notch and knob of their tips, which prevents the valve margin from destruction by concentrating force there during anterior boring.

At this stage, the anterior valve margin must open widely even though the posterior margin has a relatively narrow gape. This can be accomplished by the obliquely running **PAM**. When the **PAM** contracts, the postero-dorsal margin of the left valve slides inside the right, so that the anterior valve margin can open widely. The overlapping of the postero-dorsal parts of the two valves extends to an angle of about 30 degrees, but gradually be-

comes inconspicuous with growth and is almost invisible by the end of this stage.

When the anterior valve margin opens widely due to contraction of the **PAM**, the **AAM** located on the umbonal reflection is stretched. When the **PAM** relaxes, the **AAM** also relaxes rather than contracting, which leads to a drawing out of the left valve from inside the right valve. At the same time, the foot is extended and the shell leaves the burrow wall. This is followed by a step in which the two muscles contract simultaneously, and the valves close. During this step, the foot contracts to press the shell against the burrow heading.

Stage C: A series of boring movements begins with opening the anterior valve margin by rotation around the dorso-ventral axis due to contraction of the **PAM**; this movement is identical to that seen in stage B (Figure 7C). This is followed by opening of the ventral valve margin as a result of a change in rotation axis from dorso-ventral to longitudinal. Rotation around the longitudinal axis (hinge line) is effected by contraction of the **AAM-P**, which is located dorsal to the hinge axis and acts as an abductor muscle (Figure 8C).

During this series of movements, the ventral parts of the valves, as well as the anterior parts, abrade the burrow wall (antero-ventral boring). During this boring motion, the **AAM-A** is stretched. The **AAM-A** retains the original

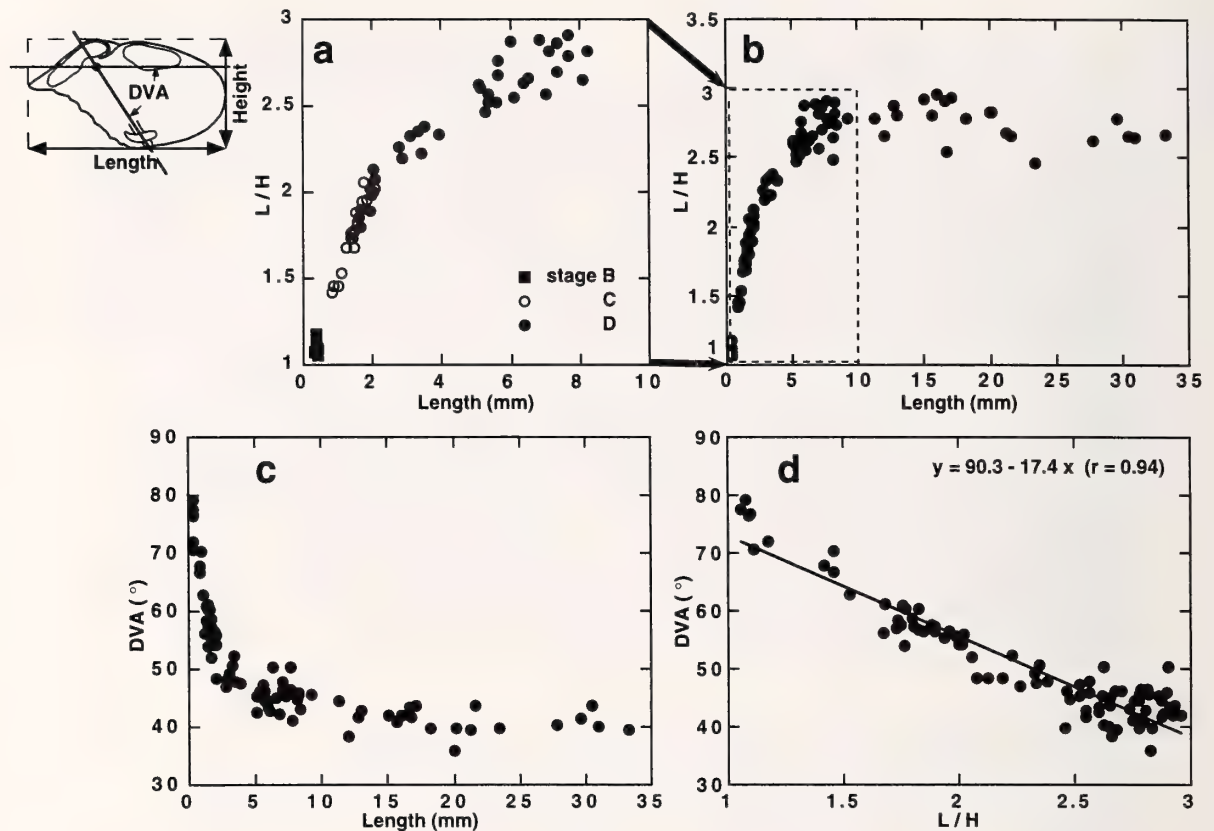


Figure 5

Allometric shell growth in stage B, C, and D of *Barnea manilensis* from Cape Taito, Chiba, Japan (UMUT RM 27595, 27596). 5a, b = shell length (L)/height (H) ratio plotted against length (L); 5a shows the enlarged dashed area of 5b. 5c = angle (DVA) between longitudinal axis and dorso-ventral axis plotted against length (L). 5d = DVA angle plotted against shell shape (L/H).

function of the **AAM**, i.e., closure of the valves, at this stage and afterward. The ventral shell opening becomes gradually wider with growth. The posterior siphonal gape also becomes wider with growth and enables the anterior margin to open without overlapping the postero-dorsal margin.

The ligament becomes vestigial and loses its function during this stage. The **AAM-P** takes over the function of the ligament to connect the two valves.

In stages C and D of *B. manilensis*, the **AAM-P** and the **PAM** are mainly used to open the valves ventrally and anteriorly, respectively. The contraction of the **VAM** aids valve closure (Röder, 1977), which in most bivalves is done by contracting the **AAM** and the **PAM** synchronously. The **VAM** gradually takes over the role of the ventral condyle to hold the valves together with the dorsal condyle when the valves rotate around the dorso-ventral axis.

Stage D: When the ventral valve margin opens by contraction of the **AAM-P**, all external surfaces of both

valves abrade the burrow wall (ventral boring) (Figure 7D). At the same time, rotation around the prosocline dorso-ventral axis occurs by contraction of the **PAM** that leads to the valves being somewhat open anteriorly in addition to their being open ventrally. The ventral valve margins, having no ventral condyles, no longer contact each other, in contrast to earlier stages.

DISCUSSION

Shell Outline and Boring Style

This study demonstrates that *Barnea manilensis* changes its boring behavior throughout ontogeny. Early round-shelled juveniles employ anterior boring, whereas, after going through intermediate shell morphologies and boring styles, the older and larger long-shelled individuals finally employ ventral boring. Other borers among the Pholadacea also employ anterior and ventral boring. In the pholads, there is a close relationship between boring style and shell morphology (Röder, 1977; Seilacher,

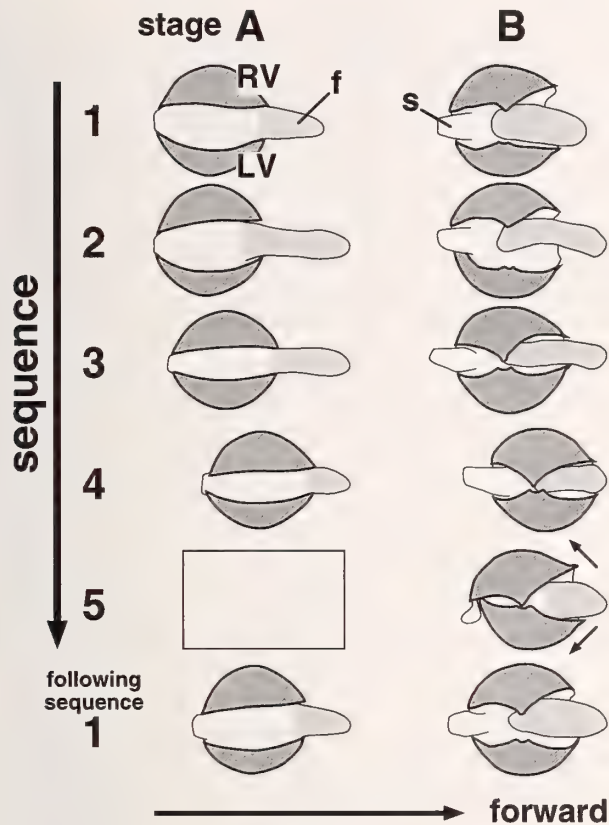


Figure 6

Diagrammatic ventral view of crawling cycles in stages A and B of *Barnea manilensis*. LV = left valve; RV = right valve; f = foot; s = siphon.

1985). In general, pholads having short shells, thick knobby ventral condyles, and large **PAMs** are anterior borers, because these features open the anterior valve margin for rotation around the dorso-ventral axis to achieve boring. On the other hand, pholads having long shells with narrow pedal gapes and large **AAM-Ps** are ventral borers because these features open the ventral margin for rotation around the longitudinal axis to produce boring. There are intermediate forms and boring styles between the extremes of anterior and ventral boring.

Anterior Boring vs. Ventral Boring

Many species of Pholadacea employ anterior boring throughout life, such as *Teredo*, and others such as *Barnea manilensis* begin with the early juvenile anterior boring and change toward ventral boring with growth. So far as the author knows, the reverse order of development has never been reported among the Pholadacea. It is probable that all Pholadacea species employ anterior boring as early juveniles, although not all have been observed

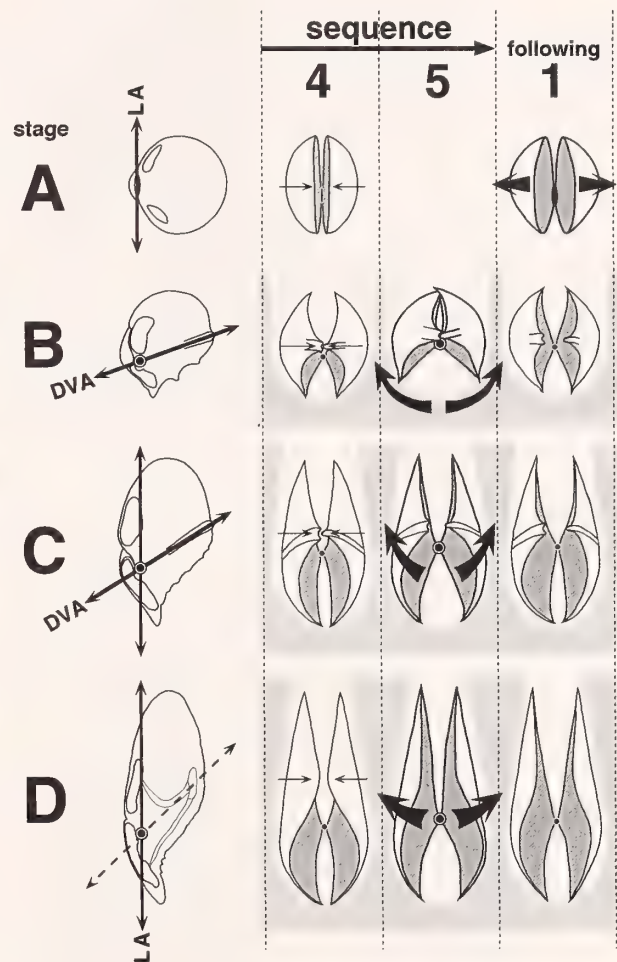


Figure 7

Diagram of boring/crawling styles in the four stages of *Barnea manilensis* development. Boring movement (sequence 5) changes from anterior boring in stage B to ventral boring in stage D. It does not yet appear in stage A. In stage A, valves open ventrally when adductor muscles relax as in sequence 1. In the stage D, valves open ventrally when the **PAM** and **AAM-P** contract as in sequence 5. Circular point = hinge or pivot. LA = longitudinal axis (hinge line); DVA = dorso-ventral axis.

to do so. Anterior boring is thought to be the primary character in boring pholads, and ventral boring is considered to be a specialized character derived from anterior boring. This conclusion is based on considerations discussed below.

Anterior borers, including juveniles of *B. manilensis* in stage B, open the anterior valve margin by rotating around the dorso-ventral axis due to contraction of the **PAM**. The only unique morphological characteristic of anterior boring is the existence of a ventral condyle that defines the ventral end of the dorso-ventral axis. The characteristics of the **PAM** are essentially those of other

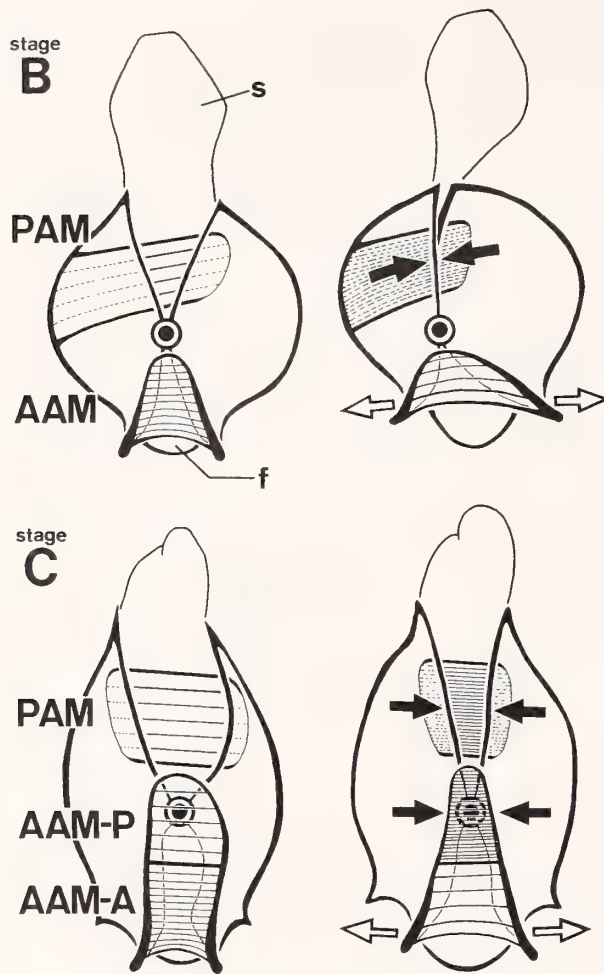


Figure 8

Diagrammatic dorsal view of the boring movement of *Barnea manilensis* in stages B and C. Circular point = dorsal pivot; s = siphon; f = foot. Closely spaced lines = contracted muscle; widely spaced lines = relaxed or stretched muscle.

bivalves, and the slender internal ligament at the dorsal end of the axis is also seen elsewhere in the Myoida. All Pholadacea have a ventral condyle, at least during the juvenile stage immediately after metamorphosis. The ventral condyle either disappears or continues to develop depending on the boring style of the species.

All Teredinidae species are anterior borers that have a prominent ventral condyle (Turner, 1969), which appears immediately after metamorphosis and then develops into a thick knob in larger individuals (Lebour, 1946; Sullivan, 1948; Turner & Johnson, 1971; Fuller et al., 1989; Tan et al., 1993). The members of the Pholadidae, except for the Pholadinae, also possess a ventral condyle (Turner, 1969) throughout life. In three modern genera of Pholadinae, i.e., *Barnea*, *Cyrtopleura*, and *Pholas*, the ventral condyle is invariably lost in larger shells (Turner, 1969).

These genera are ventral borers (Röder, 1977). Although the ventral condyle disappears from *B. manilensis* in stage D, juveniles in stages B and C still possess it. *Zirfaea* is an antero-ventral borer in larger individuals (Nair & Ansell, 1968) and is the only genus in the Pholadinae which retains a ventral condyle throughout life. Its umbonal-ventral sulcus becomes invisible with growth (Turner, 1954), which is the same change seen in *B. manilensis* during its transition from stage C to D. This suggests that the absence of a ventral condyle in other Pholadinae is ascribable to its secondary disappearance during growth and elongation of the shell.

On the other hand, some Pholadacea, including *B. manilensis* in stage D, achieve ventral boring by opening the ventral valve margin with the help of the AAM-P. The AAM-P is located on the dorsal side of the hinge axis, and acts as the abductor muscle (Röder, 1977; Seilacher, 1985). In *B. manilensis*, the umbonal reflection bearing the AAM-P gradually moves to the dorsal side of the dorsal condyle (hinge axis) during the post-larval boring stages. Similar ontogenetic development of the AAM-P is observed in *Zirfaea crispata* (Sullivan, 1948; Turner, 1954). The ligament and chondrophore structure in *B. manilensis* are well developed immediately after metamorphosis when anterior boring is effected, but rapidly become vestigial with growth, and *B. manilensis* becomes a ventral borer. Similar reduction in these structures is observed in the ventral borer *Pholas dactylus* (Purchon, 1955; Le Pennec, 1980) and the antero-ventral borer *Z. crispata* (Sullivan, 1948; Purchon, 1955). Ventral boring does not begin until the AAM-P assumes the function of the ligament to connect and open the valves. Pholads that have not developed an AAM-P employ anterior boring, as in *Teredo* (Miller, 1924). The structures needed for ventral boring are more specialized than those for anterior boring.

Diversification of Boring Styles in the Pholadacea

Some workers have concluded that anterior-boring pholads specialized from ventral borers (Nair & Ansell, 1968; Seilacher, 1985). This idea is based on the assumption that borers primarily use the common burrowing mechanism of bivalves for boring in rock as for opening and closing the ventral valve margin and rotating around the longitudinal axis of the shell. However, the ventral opening for boring in pholads appears in a later developmental stage than does the opening for normal burrowing and early juvenile movement. In addition, the opening mechanism needed for boring is quite different from that needed for more ordinary movements. In ordinary burrowing bivalves, when both adductor muscles relax, the ventral valve margin opens by elastic rebound of the ligament and insertion of the foot (Trueman, 1964), which is derived from the crawling sequence of the pediveliger stage (Nelson, 1924; Prytherch, 1934; Quayle,

1949; Carriker, 1961; Cranfield, 1973). In pholads, however, the opening of the ventral valve margin and rotation around the longitudinal axis is achieved by contraction of the AAM-P, located on the dorsal side of the hinge.

The rotation of valves for both anterior and ventral boring is a movement newly added at the time of metamorphosis to the crawling sequence of the pediveliger stage, as observed in the transition from stage A to B of *Barnea manilensis*. This new motion is added to the crawling sequence just after contraction of the foot and before relaxation of the muscles. This motion first appears as a rotation around the dorso-ventral axis during the early juvenile stages, then gradually changes into longitudinal motion with growth.

All pholads are thought to develop anterior boring immediately after metamorphosis, irrespective of the boring style in their later developmental stages. Anterior boring is evidently a primary character common to boring pholads. Some pholads, such as *Teredo*, retain anterior boring throughout life, whereas others, such as *Barnea*, shift to ventral boring.

This study suggests that anterior boring appeared early in the phylogeny of pholads, and that ventral boring evolved later. This interpretation is supported by the fossil record, in which the anterior borers appeared earlier than ventral borers. The oldest pholad, *Teredo australis* (Moore, 1870), is an anterior borer recorded from the Middle Jurassic. *Opertochasma* (Martesiinae) and *Turnus* (subfamily uncertain) probably are anterior borers known from the Upper Jurassic (see Kelly, 1988). Further, the ichnogenus *Teredolites*, which consists of burrows made in wood by anterior boring (as in modern *Teredo* or *Martesia*), is known from the Jurassic (Kelly & Bromley, 1984). The oldest ventral borers, on the other hand, the Pholadinae *Pholas? scaphoides* (Stephenson, 1952) and *Barnea saulae* (Kennedy, 1993), are recorded only as far back as the Late Cretaceous. Based on the fossil record, Kelly (1988) suggested that mud borers (ventral borers as used herein) may have been derived secondarily from wood borers (anterior borers). My observations on the ontogenetic development of boring behavior in *B. manilensis* add new insight into the primordial character of anterior boring.

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A New Species of Gastropod of the Genus *Trophon* Montfort, 1810 (Mollusca: Gastropoda: Muricidae) from Subantarctic Waters

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Abstract. *Trophon veronicae*, a new species of gastropod belonging to the subfamily Trophoninae, is described from deep waters off southern Chile, Argentina, and subantarctic seas. This new species is similar to *T. mucrone* Houart from South Brazilian waters. *Trophon veronicae* sp. nov. can be distinguished from *T. mucrone*, which is known only from the shell, by its larger size and more slender profile. In addition, the siphonal canal of *T. veronicae* is very long and curved. The radula and penis of *T. veronicae* are described and illustrated with SEM photographs.

INTRODUCTION

The genus *Trophon* Montfort, 1810, comprises a group of predatory marine neogastropods that are endemic to South American and Antarctic waters. The genus includes approximately 35 Recent species inhabiting Antarctic waters and ranging as far north as Rio de Janeiro, Brazil. Most of these species live in water less than 500 m deep; several range to 1000 m, and very few live deeper. *Trophon veronicae* sp. nov. is described from bathyal depths of the subantarctic waters off Chile and Argentina.

MATERIALS AND METHODS

The holotype and paratypes are from material collected by the United States Antarctic Program on several different cruises, plus one additional specimen housed in the collection of the United States National Museum of Natural History (USNM). One paratype has been deposited in the malacological collection of the Departamento de Zoología Invertebrados, Museo de La Plata, Argentina (MLP-5363).

The radulae were prepared according to the method described by Solem (1972) and observed under the scanning electron microscope (SEM). The type series contains two specimens with soft parts. These were dissected; the penis was critical point dried, coated with Au-Pd, and photographed under the SEM.

Shell ultrastructure data were procured from freshly fractured shell fragments of two specimens. The fragments were cut out from the central lip of the last whorl, and also were examined by SEM.

SYSTEMATICS

Class Gastropoda Cuvier, 1797

Order Neogastropoda Wenz, 1938

Family MURICIDAE Rafinesque, 1815

Subfamily TROPHONINAE Cossmann, 1903

Genus *Trophon* Montfort, 1810

Type species: *Murex magellanicus* Gmelin, 1791 (= *Trophon geversianus* (Pallas, 1774)) by original designation.

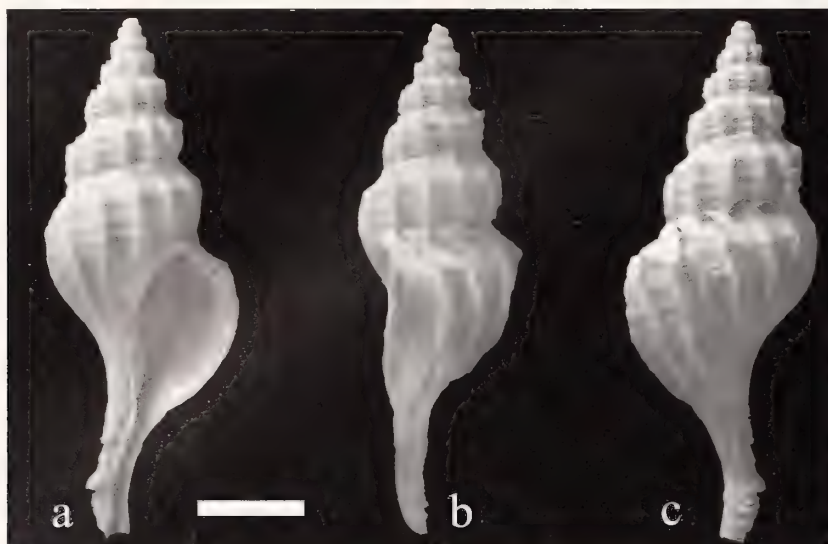
Trophon veronicae Pastorino, sp. nov.

(Figures 1–12)

Type locality: Eltanin Cruise 25 stat. 325, Blake trawl, off southern Chile 46°00'S, 83°59'W, 742 m, collected on 9 October 1966.

Type material: Holotype and 11 paratypes in USNM, 1 paratype in MLP.

Material examined: Holotype, USNM 880195, Eltanin Cruise 25 sta. 325, 46°00'S, 83°59'W, Blake trawl, 742 m; 5 paratypes, USNM 880196, Eltanin Cruise 25, sta. 326, 46°04'S, 83°55'W, Blake trawl, collected on 9 October 1966, 298 m; 5 paratypes, USNM 870370, Eltanin Cruise 9, sta. 661, 50°32'S, 43°32'W, Menzies trawl, collected on 11 August 1963, 1272–1281 m; 1 paratype, USNM 97071, 53°01'S, 73°42'W, 675 m; 1 paratype, MLP 5363, Eltanin Cruise 25 sta. 325, 46°00'S, 83°59'W, Blake trawl, collected on 9 October 1966, 742 m; 2 broken specimens, USNM 880197, Eltanin Cruise 25, sta. 326, 50°32'S, 43°32'W, Blake trawl, collected on 9 October 1966, 298 m.



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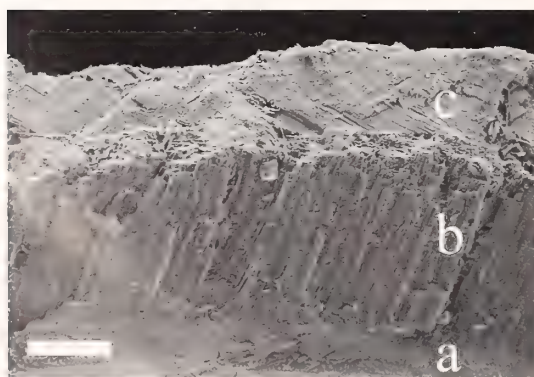
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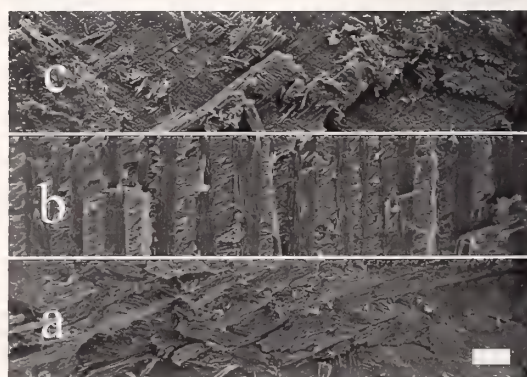
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Distribution: Known from off southern Chile, the Strait of Magellan, and off South Georgia Islands in 298–1272 m (Figure 13).

Etymology: This species is dedicated to Verónica A. Ivanov.

Description: Shell large (to 52 mm), elongate, biconic, fusiform, very slender, chalky; protoconch worn on all but one specimen, of at least two and a half whorls; teleoconch of seven sharply shouldered whorls, spire very high, about one-third of total shell length. Spire angle about 45°; suture abutting; subsutural ramp steeply inclined; aperture subovoidal, interior glossy white; anterior siphonal canal very long (same length as aperture), narrow, curved, open; posterior canal weakly demarcated in some specimens; umbilicus absent; outer lip rounded with reflected edges; inner lip gently curved, adpressed. Axial sculpture of 12–13 regular, weakly lamellose varices on last whorl. Regular growth lines present throughout shell. Spiral ornamentation consisting of three cords, always below shoulder, that become obsolete over last whorl; entire shell surface covered by regular, delicate spiral threads.

Shell ultrastructure composed of three layers (Figures 5, 6); innermost layer (0.1 shell thickness), composed of collabrally aligned crossed lamellar aragonite, middle layer thick (0.45 shell thickness) of crossed lamellar aragonite with crystal planes oriented perpendicular to growing edge; outer layer thick (0.45 shell thickness) with collabral lamellae of crossed lamellar aragonite.

Operculum (Figure 11) oval, subpolygonal, with terminal nucleus abraded in adult specimens. External surface covered by concentric, irregular, often overlapping growth lines. Inner surface with 15–20 regularly rounded and continuous growth lines; very heavily callused, glazed rim present in adult specimens.

Animal small relative to shell. Mantle large, mantle roof thin. Cephalic tentacles medium in size, blunt, with rounded large black eyes; mantle edge thickened, smooth, siphon long; pallial organs arranged as in other rachiglossans; dark osphradium more than half of ctenidium length, thin, slightly asymmetrical, with 75–80 leaflets per side; ctenidium is twice as wide as osphradium, containing 140–150 triangular leaflets. Hypobranchial gland brownish and inconspicuous, rectum and large penis to right of hypobranchial gland.

Penis large, more than four times length size of ten-

tacles, wide, flat; papilla conical, flanked by two flaplike extensions of the penis edge.

Pleurembolic proboscis short, broad. Radular ribbon small, extending beyond rear of buccal mass. Esophagus loops toward left side, where it receives embedded ducts of salivary glands just anterior to valve of Leiblein. Esophagus joined by brown, well-developed, gland Framboisse just posterior to the nerve ring. Large salivary glands envelop retracted proboscis. Accessory salivary glands small, embedded in salivary glands. Gland of Leiblein conspicuous, overlays esophagus, ends posteriorly in a short blind duct with a small ampulla.

Rachiglossan radula (Figures 7, 8, 10) with rachidian teeth very wide (200 μ m), central cusp thin, large; lateral cusps half size of central cusp, pointing outward, with inner edge slightly curved; denticle between central and lateral cusp very small, thin, almost obsolete. Base of rachidian tooth strongly curved. Marginal area large, smooth. Lateral teeth with single, long cusps along outer edge of narrow basal plate.

Juvenile specimens have proportionally larger inner denticles and thinner rachidian teeth (Figure 10). In addition, the base of the rachidian teeth of juveniles is more curved. Lateral teeth are shorter, thicker. In lateral view both stages have rachidian teeth with a triangular profile.

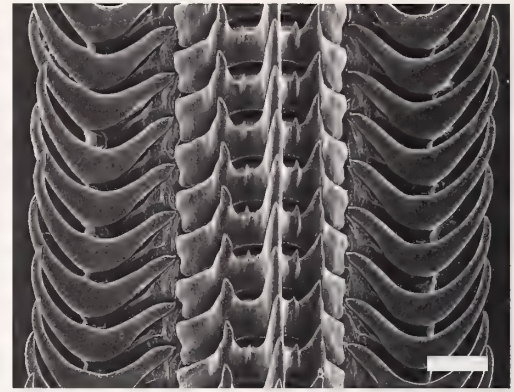
Remarks: The whole complex of the southern South American and Antarctic Trophoninae includes at least 50 described species in addition to several still undescribed. Two groups are clearly differentiated by radular characters. The Patagonian group has complex radulae with the rachidian teeth bearing three cusps, a typical denticle on the inner edge of the lateral cusps, and several denticles along the outer side. Two very developed marginal cusps are also present. In contrast, the Antarctic group has several types of radulae, but always within the same pattern of a tricuspid, rachidian with an inner, intermediate denticle rising from the base of this tooth, and without marginal cusps. Regarding shell characters, the protoconch on most of the Patagonian representatives is in general asymmetrical and paucispiral. The Antarctic species present a variety of morphologies, including that of *T. veronicae*. Compared with the South American group, this new species most closely resembles *T. mucrone* Houart, 1991, from the Abrolhos Archipelago of southeastern Brazil, but is almost twice the length and width of *T.*

Figures 1–6

Trophon veronicae Pastorino, sp. nov. 1, a–c holotype USNM 880195 2. Paratype MLP 5363, scale bar = 1 cm; 3. Paratype USNM 880196, protoconch apical view, SEM not coated, scale bar = 200 μ . 4. Same specimen side view, SEM not coated, scale bar = 200 μ . 5. Shell ultrastructure, a. innermost aragonitic layer, b. medium aragonitic layer, c. external aragonitic layer, SEM coated, scale bar = 100 μ . 6. Detail of the layers in Figure 5, scale bar = 2 μ .



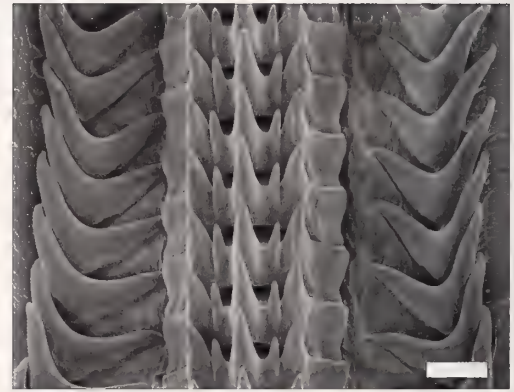
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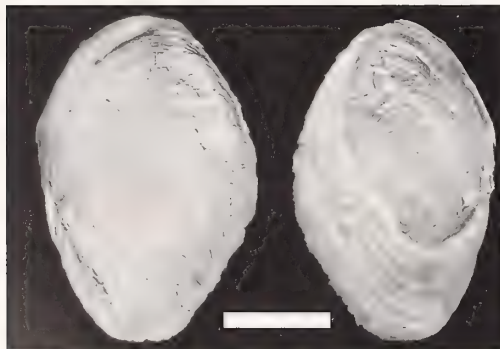
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Figures 7–12

Trophon veronicae Pastorino, sp. nov. 7–8. Radula, side view; scale bar = 80 μ ; SEM USNM 880195; 9. Penis, scale bar = 300 μ . 10. Radula, juvenile specimen, scale bar = 20 μ . 11. Operculum dorsal and ventral view, scale bar = 4 cm. 12. Penis side view, scale bar = 200 μ .

mucrone (Table 1). *Trophon veronicae* is also narrower and much more slender than *T. mucrone*, although the number of lamellae are similar. The siphonal canal is long and curved in *T. veronicae* but straight and shorter in *T. mucrone*.

Based on the limited material available, the number of

protoconch whorls in *T. veronicae* is almost twice that of *T. mucrone*.

In addition, the transition between protoconch and teleoconch is indistinct in the new species, whereas it is abrupt in *T. mucrone*.

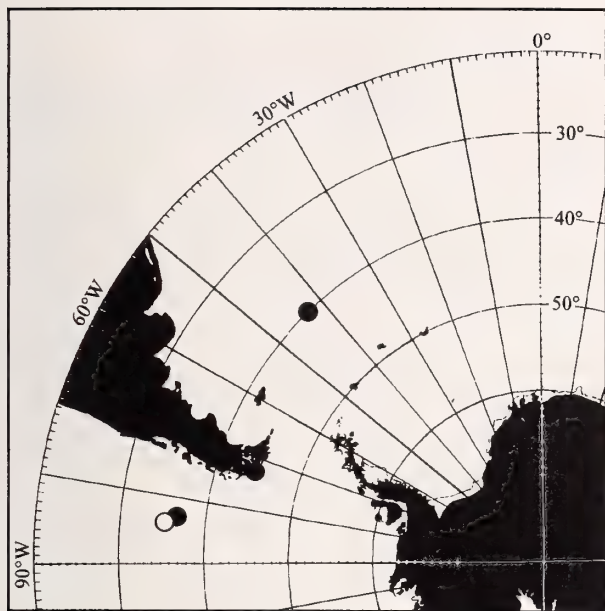


Figure 13

Localities at which *Trophon veronicae* Pastorino, sp.nov. (circles, white type locality) was collected in subantarctic waters off Chile and Argentina.

The radulae and soft parts could not be compared because they remain unknown for *T. mucrone*.

Trophon coulmanensis Smith, 1907 known from Antarctic Peninsula and Kerguelen Islands (Dell, 1990) is the only other morphologically similar species in the Antarctic. However, differences in size are significant; all the specimens known of *T. coulmanensis* are not larger than 25 mm. In addition, the protoconch of *T. coulmanensis* is asymmetrical and paucispiral, while axial lamellae of the teleoconch usually develop a peripheral spine that never appears in *T. veronicae*.

Harasewych (1984) illustrated the penes of two species

belonging to the subfamily Trophoninae: the type species of *Trophon*, *T. geversianus* (Pallas, 1774) and *Boreotrophon aculeatus* (Watson, 1882). Both species have a dorsoventrally compressed, large penis with a terminal papilla. According to Kool (1993b), *T. geversianus* also has a vas deferens as an open duct into the mantle cavity, which is very different from the closed duct of *T. veronicae*. In a very comprehensive paper about the phylogeny of the Rapaninae, Kool (1993a) described the male reproductive structures of 18 type species of accepted genera. Wu (1985) described and illustrated the penis morphology of seven species of the genus *Acanthina* Fischer, 1807. None of the species studied thus far has a penis with lateral folds enveloping the papilla, as here described.

The novel structure of the penis and radula could be indicative of a different generic position. However, the incomplete knowledge of the soft parts of other species of Trophoninae precludes extensive comparisons.

ACKNOWLEDGMENTS

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Table 1
Measurements of *T. veronicae* sp. nov. and *T. mucrone* Houart (in mm).

	Length	Width	Whorls	Lamellae on last whorl
<i>T. veronicae</i> sp. nov.				
USNM 880195 holotype	52.2	19.6	7	13
MLP 5363 paratype	48.6	19.1	7	13
USNM 880196 paratype	28.8	11.76	7	13
USNM 880196 paratype	34.0	15.0	7	18
USNM 880196 paratype	34.6	15.0	7	13
Protoconch USNM 880196	1.07	0.94	2.0–2.5	—
<i>T. mucrone</i> Houart				
MNHN holotype	26.5	11	7	12
Protoconch —	0.86	0.71	1.5–1.75	—

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Observations on Epithelial Mucocytes in the Sole of *Patella* Species and *Littorina littorea* (Linnaeus, 1758)

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Abstract. The sole epithelia of populations of *Patella vulgata* Linnaeus, *P. ulyssiponensis* Gmelin, and *P. depressa* Pennant, were examined by histology. There was no correlation between epithelial mucocyte density and animal size in any population. There was no significant difference in mucocyte density (mean \pm SE = $87.93 \pm 0.46 \text{ mm}^{-1}$) in *P. vulgata* populations from different heights on a moderately sheltered shore. Mucocyte density in *P. vulgata* varied with wave exposure, but not in any consistent pattern. The other patellids examined showed variation in pedal mucocyte density, but it was difficult to identify the causes of this variation. Electron microscopy revealed very similar microvillous epithelial layers in both *P. vulgata* and *Littorina littorea* (Linnaeus). Epithelial mucocytes could be seen discharging their contents onto the sole. Goblet cells contained membrane-bound packages ($\sim 0.2\text{--}1 \mu\text{m}$) of mucus (or mucin), similar to those found in terrestrial slugs.

INTRODUCTION

Histological examination of the gastropod epidermis has attracted much attention (see Simkiss & Wilbur, 1977; Grenon & Walker, 1978; Shirbhate & Cook, 1987 for reviews), as have the functions of the gastropod epidermis, such as respiration (Zaaijer & Wolverkamp, 1958; Jones, 1961), osmoregulation (van Aardt, 1968; Greenaway, 1970), and tenacity (Grenon & Walker, 1981). There has, however, been little attempt to relate such function to the detailed structure of the epidermis. Here I make some observations by microscopy on the structure of the epidermis of the foot in intertidal mollusks (*Patella* species and the periwinkle *Littorina littorea* [Linnaeus, 1758]) and attempt to relate these observations to the functioning of the mucocytes present. Mucus secretion is a characteristic feature of the molluscan epidermis and is important in a wide range of physiological processes (see Davies & Hawkins, 1998).

Grenon & Walker (1978) described histologically and biochemically the structure of the foot and pedal glandular system of *Patella vulgata* Linnaeus, 1758, and proposed functions for each of nine gland types (*P1* to *P9*) identified. Six of the gland types release their secretions onto the foot sole and three onto the side-wall. The sole epithelium consists of three cell types: non-ciliated cells, ciliated cells, and *P9* goblet cells (mucocytes). Of the other pedal gland types, the remainder, except the large anterior pedal gland, are subepithelial and release their contents via necks through the epithelium. The *P9* mucocytes are randomly distributed throughout the foot, ex-

cept in the peripheral region (Grenon & Walker, 1978) and are by far the most common type of mucocyte present (personal observation). Such epithelial goblet cells are present in many prosobranchs (Fretter & Graham, 1994), and through studies of their secretions (Hunt, 1973; Grenon & Walker, 1978), their function has been surmised as locomotory (Grenon & Walker, 1978). However, locomotory mucus is probably secreted mostly by the marginal gland in the anterior marginal groove (Fretter & Graham, 1994; Grenon & Walker, 1978), providing a layer of mucus over which the foot can pass. The *P9* glands are unlikely to provide a surface lubricant or protective layer as their density is much greater in the sole of the foot than in areas where these functions are more important, such as the side-wall (Grenon & Walker, 1978). The *P9* glands may function in adhesion, and Grenon & Walker (1978) suggested some pedal glands secrete a highly viscous mucus for adhesive function while others secrete a less viscous mucus for locomotory purposes. The acid glycosaminoglycan secretion of the *P9* glands (Hunt, 1973; Grenon & Walker, 1978) is indicative of high viscosity in aqueous solution (Hunt, 1973), and this suggests an adhesive function, although this was not considered so by Grenon & Walker who argued that adhesive was produced by the more acidic mucin of other, subepithelial glands. Denny & Gosline (1980), however, demonstrated plastic viscoelastic properties of a single pedal mucus of *Ariolimax columbianus* (Gould, 1851), allowing both locomotory and adhesive function.

MATERIALS AND METHODS

Histology

Twenty-five *Patella vulgata* each were collected from horizontal surfaces at high-, mid-, and low-shore on a

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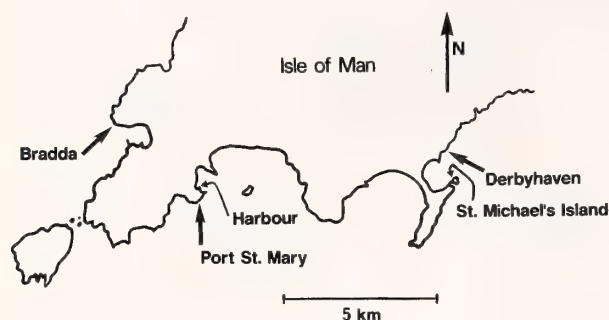


Figure 1

Sample sites in the south of the Isle of Man, Irish Sea.

moderately sheltered (rated five on Ballantine's 1961 exposure scale) rocky shore at Derbyhaven, Isle of Man (Grid Reference SC 294 685; fig. 1). Further samples of 10 to 15 *P. vulgata* were collected from horizontal surfaces each at mid-shore on the semi-exposed shore at Port St. Mary, Isle of Man (Grid Reference SC 208 669; four on Ballantine's 1961 scale), the very sheltered shore at St. Michael's Island, Isle of Man (Grid Reference SC 294 674; Ballantine, seven), and the exposed shore at Bradda, Isle of Man (Grid Reference SC 183 699; Ballantine, three) (Figure 1). Fifteen *P. ulyssiponensis* Gmelin, 1791, were also collected from horizontal surfaces at low-shore at Port St. Mary. An additional five *P. ulyssiponensis* were collected from shallow rock pools, and 21 *P. depressa* Pennant, 1771, from almost vertical surfaces from mid- to high-shore on an exposed rocky shore at Outer Hope, South Devon (Grid Reference SX 674 403). All limpets were placed in Bouin's seawater fixative. Voucher specimens have been deposited in the Marine Collection, University of Sunderland (accession numbers MAR-97-001 to MAR-97-010).

On removal from the fixative, the shell length of each animal was recorded and the foot removed. The foot was then cut in half laterally and one half prepared for histological examination by dehydration and clearing in xylene. Serial transverse sections in wax were made from the cut edge at 8 μm . The second, twenty-fifth, and fiftieth sections were stained in 1% w/v alcian blue followed by 1% w/v eosin. Sections were examined at $\times 400$ under a light microscope and the number of epithelial mucocytes (*P9* goblet cells) were recorded at four fixed stations (determined randomly) across the width of the foot in each section. This procedure was sufficient to give stable means and standard errors of mucocyte density.

Electron Microscopy

Limpets (*Patella vulgata*) were collected from mid-shore at Derbyhaven; periwinkles (*Littorina littorea*) were collected from mid-shore at Port St. Mary harbor. The foot of each animal was cut in half laterally. One

half was then fixed in 2.5% v/v glutaraldehyde in seawater with 0.1 M sodium cacodylate for 1 hr. The tissue was then rinsed for 1 hr in buffered seawater and post-fixed in 1% v/v osmium tetroxide in buffered seawater for 2 hr. After rinsing, the tissue was dehydrated and embedded in Spurr's resin (Spurr, 1969). Sections were cut on a Reichert 4 ultramicrotome and stained for 20 min in 2% w/v uranyl acetate in 70% v/v alcohol followed by 5 min in 0.3% lead citrate in 0.1 N NaOH.

RESULTS AND DISCUSSION

Histology

An epithelial structure identical to that seen by Grenon & Walker (1978) was observed. There were three distinct cell types: non-ciliated cells, ciliated cells, and mucocytes (Grenon & Walker's *P9* cells). The necks of subepithelial mucus cells (*P8* cells), which also discharge their contents onto the pedal sole, were also observed within the epithelium. Both types of mucus cells stained with alcian blue, indicating the presence of acid glycosaminoglycan (Grenon & Walker, 1978) indicative of high-viscosity secretions (Hunt, 1973).

There was no correlation between mucocyte density and shell length for any species measured at any location, indicating that at least for type *P9* mucocytes, as the animal grows, new mucocytes are produced to maintain a specific density. Mucocyte densities recorded (expressed as mucocytes mm^{-1}) are not absolute values with respect to the sole of live *Patella*. This is because distortion of foot shape may have taken place during histological preparation. Nevertheless, mean *P9* mucocyte densities recorded (see below) lie within those recorded by Branch & Marsh (1978) in six species of *Patella* from South Africa, although Branch & Marsh sectioned at 10 μm rather than 8 μm and counted subepithelial cells.

For *P. vulgata*, differences between mean densities of mucocytes were tested by ANOVA ($F = 16.97$, $P < 0.01$) (Figure 2). Subsequent mean separation by SNK test showed no significant difference (at $P < 0.05$) in mean mucocyte density from high- to low-shore on the moderately sheltered shore at Derbyhaven (overall mean = $87.93 \text{ mm}^{-1} \pm 0.46 \text{ SE}$) (Figure 2). The relationship between mucocyte density and wave exposure is more complex. On the south and east coasts of the Isle of Man there was a significant cline in mucocyte densities from the semi-exposed shore at Port St. Mary ($95.51 \text{ mm}^{-1} \pm 1.55 \text{ SE}$) through the moderately sheltered shore at Derbyhaven to the very sheltered shore at St. Michael's Island ($80.31 \text{ mm}^{-1} \pm 1.54 \text{ SE}$). Limpets from the exposed shore at Bradda on the Manx west coast, however, had a mean mucocyte density ($80.19 \text{ mm}^{-1} \pm 1.86 \text{ SE}$) which was not significantly different to that from St. Michael's Island. For *Patella* species from South Africa, limpets secreting more mucus (with a higher density of subepithelial mucus glands) have been shown to have lower

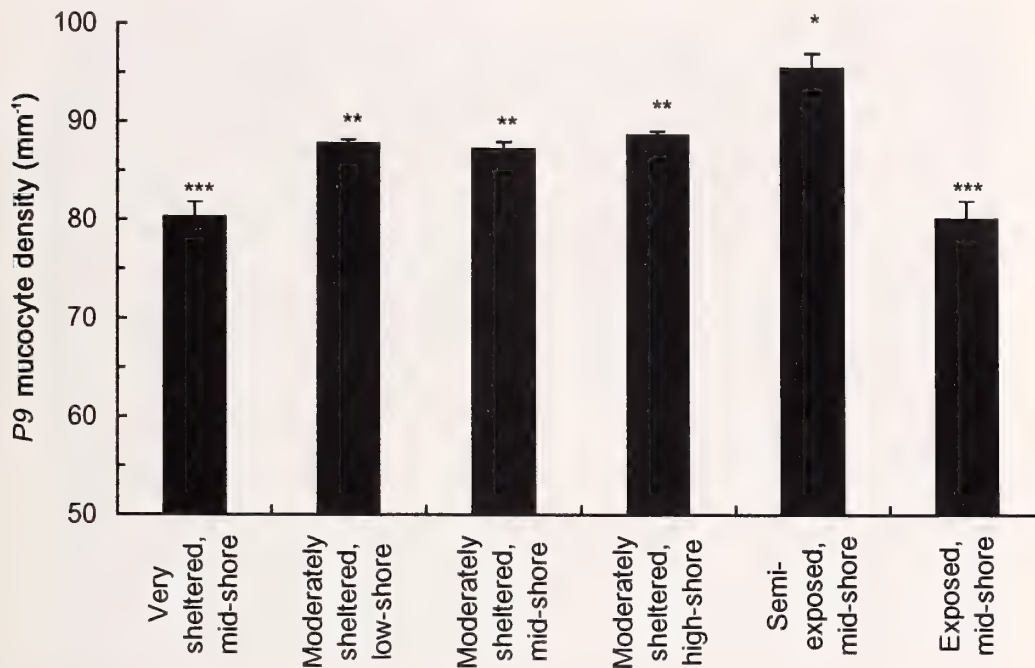


Figure 2

Mean *P9* pedal mucocyte densities (\pm SE) from six populations of *Patella vulgata* on horizontal substrata on the Isle of Man. Means with different numbers of asterisks are significantly different (SNK test, $P < 0.05$). Exposure grades refer to Ballantine (1961).

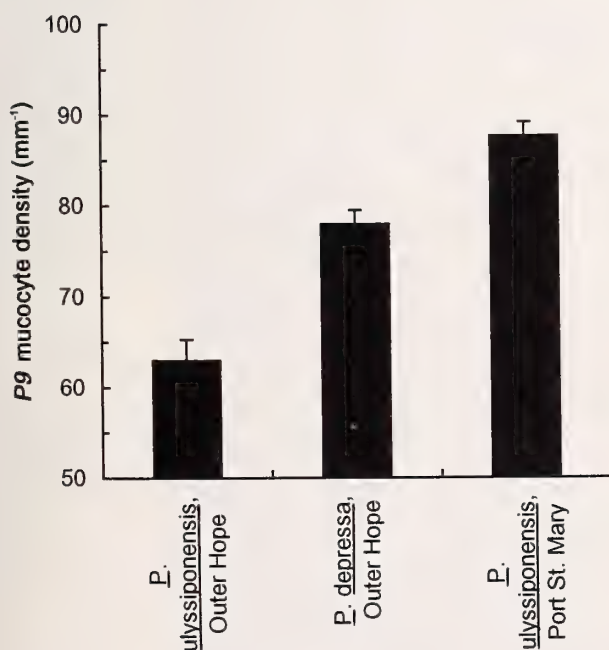
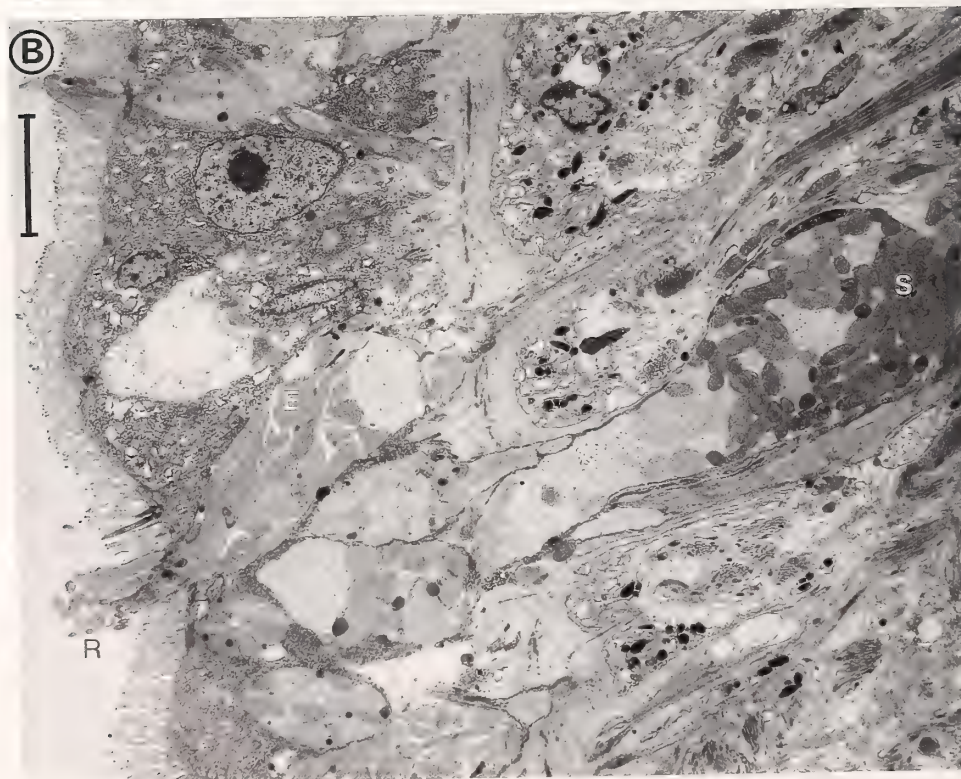
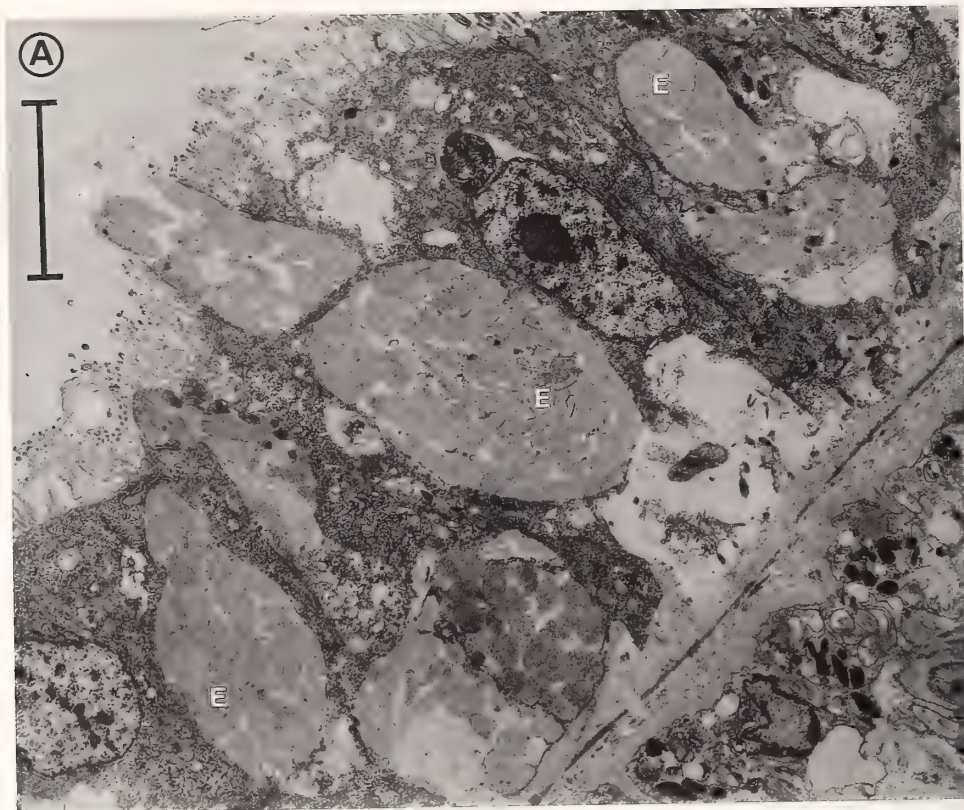


Figure 3

Mean *P9* pedal mucocyte densities (\pm SE) from *P. ulyssiponensis* and *P. depressa* populations from Outer Hope (Devon) and Port St. Mary (Isle of Man).

tenacities—suggesting mucus acts as a Stefan adhesive—and are found on relatively sheltered shores (Branch & Marsh, 1978), although this relationship did not hold for all species tested. This relationship does not occur for the Manx *P. vulgata* in terms of *P9* cells, except perhaps for those limpets on the exposed shore at Bradda which have the lowest mucocyte density of any *P. vulgata* population measured in this study. The other sites may not show sufficient variation in exposure for this to be the main factor contributing to mucocyte density, assuming that *P9* cells have an adhesive function. Hahn & Denny (1989) have shown that predation of limpets by seabirds is important at some localities and such predation may influence the adhesive capabilities of populations of limpets.

Differences in mean mucocyte density also occur interspecifically (Figure 3). On the Devon shore *P. depressa* had a higher pedal mucocyte density ($77.99 \text{ mm}^{-2} \pm 1.52 \text{ SE}$) than did *P. ulyssiponensis* ($62.96 \text{ mm}^{-2} \pm 2.34 \text{ SE}$). *P. ulyssiponensis* on the shore at Port St. Mary had a higher pedal mucocyte density ($87.78 \text{ mm}^{-2} \pm 1.51 \text{ SE}$) than did the conspecifics in Devon. The above means were not tested statistically for significant difference as the populations from which they were derived differ in more than one variable (e.g., species, exposure to wave action, microhabitat). Thus a suggestion of factors producing these results would be speculative. However, since these limpets are external fertilizers, intraspecific differ-



ences probably arise through post-settlement differential mortality or phenotypic plasticity.

Electron Microscopy

TEM revealed a foot epithelial layer of *P. vulgata* containing numerous type P9 mucocytes, some of which could be seen discharging their contents onto the epithelial surface (Figure 4A). Epithelial mucocytes in *L. littorea* were also visible discharging their contents onto the sole (Figure 4B), and subepithelial mucocytes were also present. For both species the mucus (or mucin) was contained within membrane-bound packages of ~ 0.2 – $1\ \mu\text{m}$, similar to those noted by Hunt (1970) and Zylstra (1972), although I am unable to find a reference to this phenomenon in marine snails. It is well established (e.g., Kapeleta et al., 1996) that the mucus of terrestrial slugs is released in membrane-bound packages, though these are larger, typically 5–10 μm . In slugs, environmental stresses cause the packages to burst and they then absorb water to create a functional mucus.

Epithelial gland cells may have an adhesive function and this is consistent with the presence of microvilli on the epithelial surface in both species. The microvilli increase foot surface area and suggest an absorptive or resorptive function for the epithelial cells. Perhaps adhesion is achieved by active absorption of water or specific molecules from the mucus to increase mucus viscosity (Crisp, 1973), notwithstanding the information supplied by Smith (1991, 1992) that suction is employed by some limpets. Since an increase in adhesion occurs very quickly (e.g., when a limpet is mechanically disturbed) it must be under nervous control. If the mechanism suggested by Crisp (1973) is correct, then a more thorough ultrastructural investigation of the epithelium of intertidal mollusks could reveal these nerve connections.

Although some data in this communication support the hypothesis that P9 cells are involved in adhesion, this is by no means confirmed.

ACKNOWLEDGMENTS

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Figure 4

Transmission electron micrographs showing the ultrastructure of the pedal sole of (A) *Patella vulgata* and (B) *Littorina littorea*. The epithelial layer of columnar cells lies ventral to the position of the basement membrane. All epithelial cells are microvillous and some are ciliated. Mucus is contained in packages within the vacuoles of epithelial mucocytes (E) (P9 in the limpet) and subepithelial mucocytes (S), and is released (R) onto the sole. Scale bars on (A) = 2 μm ; on (B) = 5 μm .

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NOTES, INFORMATION & NEWS

Observations on the Winter Spawning and Larval Development of the Ribbed Limpet *Lottia digitalis* (Rathke, 1833) in the San Juan Islands, Washington, USA

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Lottia digitalis (Rathke, 1833) is abundant in rocky intertidal communities from Alaska to Baja (Ricketts et al., 1985), but a complete description of its larval development has yet to be made. Koppen et al. (1996) observed *L. digitalis* development through the pre-torsional veliger stage, but did not describe later stages of development. In this note we supplement the observations of Koppen et al. (1996) by describing the development of *L. digitalis* from spawning through the onset of metamorphosis.

We collected *L. digitalis* ($n = 265$) on 10 January 1997, from False Bay, Cattle Point, Director's Cove, and Cantilever Pier on San Juan Island, Upper Puget Sound, Washington, USA, and maintained them in a 150 cm \times 60 cm running seawater table at the Friday Harbor Laboratories. Limpets spawned spontaneously in the seawater table. Eggs were collected via pipette, rinsed, and put into culture in beakers of filtered seawater, one spawn per beaker. Most eggs were already fertilized upon collection. We cultured the embryos at 8°C, ambient seawater temperature, after the method of Koppen et al. (1996). On 18 January, we added penicillin G (0.06 mg ml⁻¹) and streptomycin sulfate (0.05 mg ml⁻¹; after Chia & Koss, 1978) to our cultures in order to control bacterial growth. We used light microscopy to monitor the pattern and timing of larval development twice daily, more frequently during cleavage events.

Thirty female *L. digitalis* spawned in the seawater table between 11 and 17 January 1997. The smallest spawning female was 11.0 mm long and the largest was 20.3 mm long ($\bar{x} = 13.94$ mm, SD = 4.25 mm; $n = 20$ spawning females). The brownish green eggs had a mean diameter of 146.3 μ m (SD = 43.8 μ m; $n = 30$ unfertilized eggs). Those eggs were similar in appearance, but were significantly smaller, than those described by Koppen et al. (1996; $\bar{x} = 197.5$ μ m; SD = 56.6 μ m; $n = 51$ eggs; $t = 4.259$; $v = 79$; $p < 0.001$). We cannot readily explain that size dissimilarity, but we are certain that all limpets in our holding tank were *L. digitalis*. Perhaps there was

a difference in micrometer calibrations between our study and that of Koppen et al. (1996).

We also observed two male spawns. Males released pasty white strings of sperm, like those described by Koppen, et al. (1996). The spawning males were 13.0 mm and 14.0 mm long, respectively.

The proportion of limpets that spawned during our study (32 of 265 limpets—12%) was comparable to that reported by Koppen, et al. (1996; 16 of 140 limpets—11.4%). The timing and pattern of *L. digitalis* development through the pre-torsional veliger stage were similar to those reported by Koppen et al. (1996; see Table 1). Larvae reached the trochophore stage by the 31st hour after spawning. The protoconch was first visible as a shiny spot on the side of trochophore larvae opposite that of the foot rudiment (Figure 1A). Larvae became pre-torsional veligers 2.5 days after spawning (Figure 1B), and completed torsion after 5.3 days (Figure 1C). Once torsion was completed, the velum decreased in size and the foot increased in size. Eye spots appeared on the head 6.5 days after spawning, and tentacles extended through the upper surface of the velum after 8 days. By day 10, larvae crawled rather than swam in culture (Figure 1D).

Regression of the velum and crawling were two indicators that larvae were undergoing metamorphosis. We were not able to observe the completion of metamorphosis because our scheduled time at the laboratories came to an end. We believe that the *L. digitalis* we studied would complete metamorphosis within 12–14 days of spawning.

Our observations, combined with those of Koppen et

Table 1

Timing of larval development for *Lottia digitalis*, compared with data from Koppen et al. (1996).

Developmental stage	Cumulative time (hours or days)	Cumulative time Koppen et al. (1996)
Spawning	0 hr	0 hr
1st cleavage	1–2 hr	1–1.5 hr
2nd cleavage	2–4 hr	2–3 hr
3rd cleavage	3–6 hr	3–4 hr
ciliated blastula/gastrula	14 hr	14 hr
trochophore	31 hr	24 hr
pre-torsional veliger	60 hr	48–72 hr
post-torsional veliger	5.3 d	—
eyespot visible	6.5 d	—
tentacles visible	7.8 d	—
crawling on the bottom	9.8 d	—

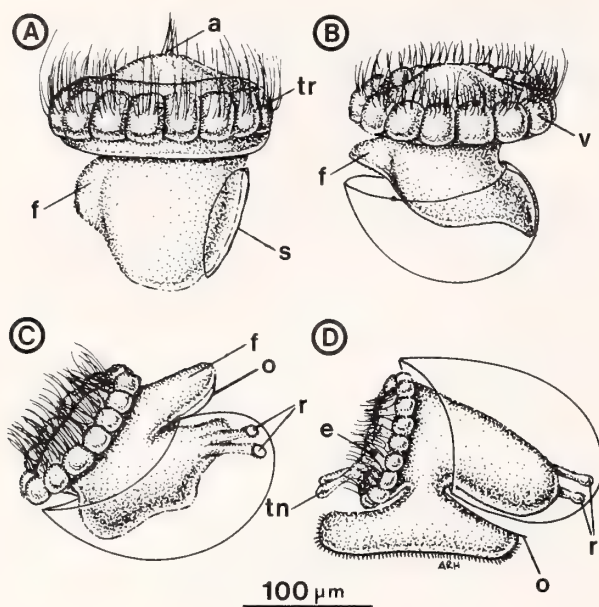


Figure 1

Developmental stages of *Lottia digitalis*. A. Late trochophore stage: a, apical tuft of cilia; tr, trochal band of cilia; f, foot rudiment; s, shell. B. Pre-torsional veliger: f, foot; v, velum. C. Post-torsional veliger: f, foot; o, operculum; r, retractor muscles. D. Crawling veliger in mid-metamorphosis: e, eye spot; tn, tentacles; r, retractor muscles; o, operculum.

al. (1996), provide the most complete description of larval development for this species to date. The two studies also show that the timing and pattern of *L. digitalis* development is similar to that of other patellogastropods of the region (Strathmann, 1989), and that a portion of San Juan *L. digitalis* populations readily spawn in the laboratory during the winter.

Those characteristics make *L. digitalis* a good research organism for studying the development and larval ecology of mollusks with lecithotrophic development, regardless of time of year. Further studies are needed in order to determine whether San Juan Island *L. digitalis* spawns in the field during the winter, since *L. digitalis* reportedly spawns in the field in the San Juan Islands only during spring and summer months (Strathmann, 1987).

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The Description of a New Species of *Favartia* (*Murexiella*) from the South Pacific Ocean

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Introduction

Dr. Donald R. Shasky of Oceanside, California, made available to us for study some specimens of a muricid he collected offshore at Pointe Taharaa, Papara and Motu Martin, all Tahiti, Society Islands. We have determined them to be an undescribed *Favartia* (*Murexiella*) species.

There has been considerable difference of opinion in recent years concerning the placement of *Favartia* Jousseaume, 1880, and *Murexiella* Clench & Pérez-Farfante, 1945. Vokes (1968) and Emerson & D'Attilio (1970) illustrated the radula of the type of *Murexiella*, *M. hidalgoi* Crosse, 1869, and Ponder (1972) illustrated the radula and operculum of the type of *Favartia*, *F. brevicula* Sowerby, 1834, and he determined that "*Murexiella* can be regarded, at best, as being only subgenerically distinct from *Favartia*." We follow Ponder (1972) in considering *Murexiella* as a subgenus of *Favartia*.

The following abbreviations for institutions and collections are used in the text: National Museum of Natural History, Smithsonian Institution (USNM); Santa Barbara Museum of Natural History (SBMNH); San Diego Natural History Museum (SDNHM); Shasky Collection (SC); Hertz Collection (HC); Myers Collection (MC).

Systematics

MURICIDAE Rafinesque, 1815

MURICOPSINAE Radwin & D'Attilio, 1971

Genus *Favartia* Jousseaume, 1880

Subgenus *Murexiella* Clench & Pérez Farfante, 1945

Favartia (*Murexiella*) *lillouxi* Myers & Hertz, sp. nov.

(Figures 1–4)

Description: Shell small, maximum size 13.8 × 8.4 mm, fusiform, spire elongate. Protoconch with 1½ white, bul-

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bous nuclear whorls somewhat oblique, tip immersed, buttressed on last half whorl. Teleoconch of five whorls, suture moderately impressed, six varices on body whorl, six on penultimate whorl. Leading edge of varix foliose, deeply excavated abaperturally. Aperture ovate, outer lip crenulate reflecting spiral cords, inner lip erect along entire length, smooth within, anal sulcus weakly defined. Siphonal canal moderately long, open to right, tubelike, sharply recurved, two-three well-preserved canal terminations on siphonal fasciole. Spiral sculpture of two cords on each of first four whorls, body whorl with five strong cords followed by gap and one strong cord on canal, bifid terminally. All cords, webbed between, terminating in open spines at varices; cords on first and second whorls with two spiral grooves along length, third, fourth and canal cords with one groove. Remnants of appressed scales on cords. Subadult uneroded specimens scaly with fine incised lines covering scales visible under magnification. Radula and operculum unknown, specimens dead collected. Color ochre to light brown.

Type locality: Off Pointe Taharaa, Tahiti, Society Islands (17°45.2'S, 149°30.4'W) in 11–22 meters.

Type material: All type material collected within a mile of the type locality (*vide* D. R. Shasky). Holotype: 12.5 mm × 8.7 mm (SBMNH 144184), off Pointe Taharaa, in 11–22 m, collected from 21–24 October 1996, leg. D. R. Shasky; Paratypes: A, 5.2 × 3.9 mm (USNM 880251), Papara, Tahiti, on coral in 0.6–1.5 m, 16 October 1996, leg. D. R. Shasky; B (broken specimen, spire missing), 7.8 mm width of body whorl (SDNHM 93557); C, 13.8 × 8.4 mm; D, 9.7 × 6.6 mm; E, 8.8 × 6.6 (broken canal); (B–E off Pointe Taharaa, collected in 11–22 m, from 21–24 October 1996, leg. D. R. Shasky & P. Lilloux (SC); F, 5.2 × 3.3 mm, same data as B–E (HC); G, 3.2 × 2.2 mm, Pointe Taharaa, in 11–22 m, 14–21 October 1996, leg. D. R. Shasky (SC); H, 4.4 × 2.7 mm, same data as G (MC); I, 11.8 mm × 7.3 mm, Pointe Taharaa, in 11–22 m, 21–24 October 1996, leg. D. R. Shasky & P. Lilloux (SC); J, 9.7 × 6.9 mm, in 15 m, Motu Martin, Tahiti, 14 October 1996, leg. D. R. Shasky (SC).

Other material studied: Two broken specimens off Motu Martin, Tahiti, in 15 m, 14 October 1996, leg. D. R. Shasky (SC).

Distribution: *Favartia (Murexiella) lillouxi* is known only from Tahiti, Society Islands.

Etymology: This species is named in honor of Patrick Lilloux of Mahina, Tahiti, a longtime friend and dive buddy of D. R. Shasky, who contributed several of the type specimens.

Discussion: This species closely resembles *Favartia (Murexiella) rosamiae* D'Attilio & Myers, 1985, but differs in the protoconch, number of varices, and spiral sculpture. The protoconch of *F. (M.) lillouxi* has 1½ bulbous whorls whereas *F. (M.) rosamiae* has 3¼ conical whorls. *Favartia (M.) lillouxi* has six varices on the body whorl and *F. (M.) rosamiae* has four. There are five spiral cords on the body whorl and one on the canal in *F. (M.) lillouxi* and six on the body whorl and two on the canal in *F. (M.) rosamiae*.

Favartia (M.) lillouxi is also similar to *F. (M.) voorwindi* Ponder, 1972, a species having a shell with a broader shoulder and shorter spire. *Favartia (M.) lillouxi*, with its higher spire, is light brown with straight spines whereas *F. (M.) voorwindi* has a white shell with recurved spines.

Favartia (M.) lillouxi does not closely resemble any other western Pacific species, and our examination of worldwide *Favartia* species revealed no close congeners.

Acknowledgments

The San Diego Natural History Museum made its collections in the Scientific Library and Marine Invertebrate Department available to us. David K. Mulliner of San Diego, California, did the photography and Emily H. Vokes of Tulane University, Louisiana, reviewed the manuscript. For this we thank them. We express our appreciation to Donald R. Shasky for giving us the opportunity to describe this new *Favartia* species and for the donation of type material.

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Explanation of Figures 1 to 4

Figures 1, 2. *Favartia (Murexiella) lillouxi* Myers & Hertz, sp. nov. Holotype (SBMNH 144184), 12.5 × 8.7 mm. Off Pointe Taharaa, Tahiti, Society Islands, in 11–22 m. Leg. D. R. Shasky, 21–24 October 1996. (1) apertural view (2) dorsal view. Figures 3, 4. *Favartia (Murexiella) lillouxi* Myers & Hertz, sp. nov. Paratype A, 5.2 × 3.9 mm (USNM 880251). Papara, Tahiti, Society Islands, in 0.6–1.5 m on coral. Leg. D. R. Shasky, 16 October 1996. (3) apertural view (4) dorsal view. This specimen illustrates the protoconch and the foliaceous nature of the sculpture.



- vartia* from the West Pacific Ocean (Gastropoda: Muricidae). *The Nautilus* 99(2-3):58-61.
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High Performance Thin Layer Chromatography Determination of Carbohydrates in the Hemolymph and Digestive Gland of *Lymnaea elodes* (Gastropoda: Lymnaeidae)

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Introduction

Recent studies in our laboratory have been concerned with high performance thin layer chromatography (HPTLC) analyses of carbohydrates in the hemolymph and digestive gland-gonad (DGG) complex of medically important planorbid snails. Thus, Anderton et al. (1993) reported quantitative values for glucose and trehalose in *Biomphalaria glabrata* (Say, 1818) snails maintained on various diets, i.e., leaf lettuce, Tetramin®, and hen's egg yolk. Perez et al. (1994) studied the effects of larval trematode parasitism by *Echinostoma caproni* Richard; 1964, on sugars in *B. glabrata* and found that parasitism significantly reduced the amounts of glucose and trehalose in the hemolymph and DGGs of infected snails. Conaway et al. (1995) provided quantitative data on glucose and trehalose in several strains of *Helisoma trivolvis* (Say, 1816) snails with and without infection by larval echinostomes. Umesh et al. (1996) used HPTLC to analyze the effects of restricted diets on glucose in the hemolymph and DGG of *B. glabrata* and *H. trivolvis*. Their results showed that glucose levels were not significantly altered in snails maintained on the restricted diets described in that study.

Less information is available on the quantitative analysis of carbohydrates in lymnaeid than in planorbid snails. Lymnaeid snails play a less important role in medical malacology than do the planorbids, and this accounts in part for the relative paucity of quantitative biochemical data on the effects of diet and larval trematode parasitism

on lymnaeids. A recent study on infection of *Lymnaea elodes* (Say, 1821) in the USA with a species of *Echinostoma revolutum* (Froelich, 1802) that causes intestinal helminthiasis in wildlife and is a potential foodborne pathogen to man has been reported by Sorensen et al. (1997). Because of that report, there is renewed interest in examining various aspects of the biology and chemistry of this snail. Moreover, *L. elodes* is easy to maintain in the laboratory, attains a length of up to 3 cm within 3 months, and is a convenient experimental model for biochemical studies. A previous study on this model used HPTLC to determine neutral lipids and phospholipids in whole snail bodies (Frazer et al., 1997). The purpose of the present study was to examine by HPTLC the identity and concentrations of carbohydrates in the hemolymph and digestive gland of *L. elodes* maintained on a leaf lettuce diet.

Materials and Methods

Sugar standards were purchased from Sigma (St. Louis, Missouri, USA). Standard solutions of each sugar were prepared at concentrations of 100 ng/μL (standard solution A) and 1.00 μg/μL (standard solution B) in 70% ethanol.

Stock cultures of *L. elodes* snails were maintained at 22°C in aerated aquaria containing artificial spring water (ASW) as described in Frazer et al. (1997). Snails were fed *ad libitum* on boiled leaf lettuce. Most snails were used for analyses immediately after removal from the cultures. Some snails were maintained in ASW without food for either 4 or 12 hr prior to use for analyses (referred to below as 4-hr starved or 12-hr starved snails).

Analyses were done on pooled samples of hemolymph and digestive glands (DGs) (three snails/pool) from snails ranging between 24 and 30 mm in shell length. For hemolymph analysis, snails were blotted dry with paper towels, gently crushed, and the hemolymph from three snails collected in a 1.5 mL microcentrifuge tube. The sample was centrifuged for 3 min at 8000 g to separate the plasma from the hemocytes. One hundred μL of plasma, measured with a 100 μL Drummond (Broomall, Pennsylvania, USA) digital microdispenser, was separated from the amoebocyte pellet and placed in a new microcentrifuge tube with 500 μL of 70% ethanol. The sample was centrifuged for 5 min at 8000 g. The supernatant was combined with two washings of the pellet (100 μL of 70% ethanol for each washing) in a 2 mL vial. The sample was evaporated to dryness in a water bath (50-60°C) under a gentle stream of air and then reconstituted in 200 μL of 70% ethanol.

Snail DGs were separated from the bodies with forceps, taking care to remove and discard the gonads and digestive tract. The wet weight of the three DGs in each pool was determined (about 150 mg) before the tissues were homogenized with 500 μL of 70% ethanol in a 7

mL glass homogenizer. The homogenate was quantitatively transferred to a microcentrifuge tube and centrifuged at 8000 g for 5 min. The supernatant was removed to a 5 mL vial and combined with two washings of the pellet (100 μ L of 70% ethanol for each washing). The sample was evaporated to dryness as described for the hemolymph, but reconstituted in 400 μ L of 70% ethanol.

Boiled leaf lettuce (*Lactuca sativa*) samples (150 mg) were prepared as described for the DGs.

Qualitative TLC analysis was performed on Merck (Gibbstown, New Jersey, USA) 20 \times 10 cm HPTLC silica gel 60 CF₂₅₄ plates with preadsorbent zone and 19 channels (catalog no. 13 153). The layer was precleaned by development with dichloromethane-methanol (1:1), air dried in a fumehood, and impregnated with sodium bisulfite and citrate buffer as described earlier (Conaway et al., 1995). Standards of each sugar (2.0 μ L of standard solution A) and samples (5.0 and 7.0 μ L of reconstituted hemolymph and 2.0 and 6.0 μ L of DG) were applied onto the preadsorbent areas of adjacent lanes using a 10 μ L Drummond digital microdispenser. Plates were developed three times in the ascending direction for a distance of 7 cm beyond the preadsorbent-silica gel interface in a paper-lined Camag (Wilmington, North Carolina, USA) twin-trough chamber with acetonitrile-deionized water (85:15) (mobile phase 1) or ethyl acetate-acetic acid-methanol-water (60:15:15:10) (mobile phase 2). The solvent was removed between developments by drying for 2 min with a hair dryer. Sugar zones were detected with 1-naphthol-sulfuric acid reagent as previously described (Anderton et al., 1993).

Sugars were identified by comparing R_f values (Umesh et al., 1996) between standard and sample zones in both mobile phases. Identities were confirmed by gas chromatography/mass spectrometry (GC/MS) in the scanning (total ion current) mode. Standards and samples were silylated with Tri-Sil® Z (Sigma, St. Louis, Missouri, USA) and chromatographed on a 30 m DB-5MS capillary column (0.25 mm i.d., 0.25 μ m film thickness of (5%-phenyl)-methylpolysiloxane stationary phase) (J&W Scientific, catalog no. 122-5532, Folsom, California, USA) in an HP6890 gas chromatograph (Hewlett-Packard Company, Palo Alto, California, USA). Standard and sample solution injection volumes were 1.0 and 2.0 μ L, respectively, helium carrier gas flow rate was 53 mL/min at 7.5 psi, the column temperature was programmed from 50°C to 280°C at 10°C/min, and the run time was 44 min.

Glucose and maltose were quantified on Whatman (Clifton, New Jersey, USA) 20 \times 20 cm TLC LK5DF silica gel plates with preadsorbent zone and 19 channels (catalog no. 4856-821). The layers were precleaned by development with dichloromethane-methanol (1:1) but were not impregnated with bisulfite and citrate buffer. For each sugar, 6.0 and 8.0 μ L of standard solution A and 1.2 and 2.4 μ L of standard solution B were applied to the same plate with the sample volumes specified above for

qualitative analysis. Plates were developed once for a distance of 18 cm with mobile phase 2. After detection, sample and standard zones were scanned at 515 nm using a Camag TLC Scanner II with a tungsten source, slit dimension settings of length 4 and width 4, and a scanning rate of 4.0 mm/sec. The maximum absorption wavelength was determined by measuring the *in situ* spectra of standard sugar zones with the spectral mode of the densitometer. The CATS-3 software linear regression program provided a calibration curve relating standard zone weights (0.600–2.40 μ g) to their computer-optimized scan areas. The analyte weights in sample zones were determined by the computer from their areas by interpolation from the calibration curve. Only calibration curves with a linear regression correlation coefficient (R) value of at least 0.93 were used for quantitative analysis; R values were typically 0.96–0.99. Sugar concentrations (mg/dL for hemolymph and weight percent for DG) were calculated as described by Anderton et al. (1993).

For five out of the six 12-hr starved hemolymph samples analyzed, the scan area of maltose in the largest spotted aliquot (15 μ L) was less than the lowest standard area. The quantity of this sugar was between zero and the experimental detection limit (2.67 mg/dL), but could not be determined since the area of the sample band was not bracketed by the standard areas. These bands were arbitrarily given a value of 1.33 mg/dL in order to include the data in statistical calculations. This value is one-half the experimental detection limit, calculated from the equation

$$\text{lowest quantifiable hemolymph sugar concentration (mg/dL)} = (L \times R)/(H \times V) \times 1/10,$$

where L is the weight of the sugar in the lowest standard aliquot (200 ng), R is the sample reconstitution volume (200 μ L), H is the highest sample aliquot spotted (15.0 μ L), and V is the original volume of sample (100 μ L).

Results

Sugars were detected as gray or blue bands on a beige background with the naphthol-sulfuric acid reagent. R_f values in the two mobile phases used for qualitative analysis of sample bands were reported by Umesh et al. (1996). The glucose standard was found to comigrate with a band in all sample chromatograms (R_f = 0.41 in mobile phase 1 and 0.70 in mobile phase 2). The maltose standard comigrated with bands in chromatograms of all DG samples, fresh fed hemolymph, and 4-hr starved hemolymph sample chromatograms, but not in the 12-hr starved hemolymph or lettuce sample (R_f = 0.22 in mobile phase 1 and 0.54 in mobile phase 2). A maltose band was not observed in the lettuce or 12-hr starved sample chromatograms above the detection limit of the analysis, 2.67 mg/dL. The fructose standard comigrated with a

Table 1

Quantitative determinations of glucose and maltose in snail digestive gland (DG) and hemolymph samples.

Snail diet	Hemolymph		DG	
	mean \pm SE		mean \pm SE	
	Glucose	Maltose	Glucose	Maltose
Fresh fed	33.8 \pm 4.9	36.1 \pm 6.0	0.0065 \pm 0.0056	0.13 \pm 0.016
4-hr starved	45.5 \pm 7.4	40.3 \pm 14	0.084 \pm 0.012	0.21 \pm 0.033
12-hr starved	43.4 \pm 9.7	5.00 \pm 4.6	0.084 \pm 0.013	0.26 \pm 0.017

n = 3–6 for each group.

band in the lettuce sample chromatogram at $R_f = 0.45$ in mobile phase 1 and 0.70 in mobile phase 2.

There were two intense bands in DG sample chromatograms that did not comigrate with any of the 13 sugar standards tested (listed in Umesh et al., 1996) ($R_f = 0.08$ and 0.06 in mobile phase 1 and 0.43 and 0.24 in mobile phase 2). There was also an unidentified band in hemolymph sample chromatograms with an R_f value less than any of the sugars we tested.

GC/MS confirmed the identity of glucose and maltose (retention times 17.85 and 25.10 min, respectively) as the major sugars in the hemolymph and DG samples. Other compounds were detected in sample chromatograms, but their mass spectra did not match those of any sugar standards. There was no peak detected at 25.30 min, the retention time of trehalose, confirming the absence of this sugar in the samples. GC/MS could not identify the compounds present in the unknown TLC bands.

Whatman LK5DF plates were more convenient to use for quantitative TLC. The sugar bands were adequately separated with only one development of mobile phase 2, and no pretreatment with sulfite and citrate buffer was necessary. Although the bands were slightly more diffuse compared to the Merck HPTLC plates, they were adequately compact and resolved to allow accurate quantification. Additionally, larger volumes of sample could be applied to the preadsorbent zones of the Whatman plates than the Merck plates. This would be important if it was necessary to apply larger volumes in order to have sample band scan areas bracketed by the standard band areas. The R_f values of glucose and maltose on LK5DF plates with mobile phase 2 were 0.48 and 0.32, respectively, while the two unidentified bands had R_f values of 0.21 and 0.10.

Quantitative results for glucose and maltose are listed in Table 1. The following populations were compared using Student's t-test: fresh fed vs. 4-hr starved, 4-hr starved vs. 12-hr starved, and fresh fed vs. 12-hr starved snails. It was found that there were no statistical differences in hemolymph and DG glucose levels as a result of starvation. However, hemolymph maltose levels were significantly lower between fresh fed and 12-hr starved

populations ($t = 3.96$, $P = 0.017$). There was also a significant increase in DG maltose levels between fresh fed and 12-hr starved samples ($t = 5.56$, $P = 0.0009$).

Glucose and sucrose were quantified in samples of boiled lettuce, and respective percentages of 0.084 \pm 0.039 and 0.014 \pm 0.0053 were found ($n = 2$). Merck HPTLC plates with triple development in mobile phase 1 rather than Whatman TLC plates with a single development in mobile phase 2 were used for these analyses because mobile phase 2 did not adequately separate glucose and sucrose bands, and sugar bands do not ascend more than half the plate on Whatman TLC plates using mobile phase 1. Sucrose standards A and B were prepared as described above for glucose, and 2.0, 6.0, and 8.0 μ L of B and 1.2 and 2.4 μ L of A (0.200–2.40 μ g) were applied to the plate along with 2.0 and 10.0 μ L of reconstituted lettuce sample solution for quantification.

Discussion

Qualitative and quantitative TLC and GC/MS have shown that glucose and maltose are the major sugars present in *L. elodes*. These results are similar to those of Umesh et al. (1996) in their analyses of sugars in *B. glabrata*. The presence of trehalose in *L. elodes*, as reported in earlier publications from our laboratory in studies on planorbid snails, i.e., Anderton et al. (1993), Perez et al. (1994), Conaway et al. (1995), was not confirmed by TLC or GC/MS in the present study.

Quantitative results indicated a statistical difference in maltose levels of *L. elodes* that were maintained without food for 12 hr. The loss of maltose from the hemolymph and subsequent increase of this sugar in the DG, as well as the increased weight percent maltose compared to glucose in the DG, suggest that maltose is an important carbohydrate for metabolism in this snail.

Regardless of the period of starvation in our study up to 12 hr there were no statistically significant changes in glucose concentrations. Veldhuijzen et al. (1976) found a sharp decline in body tissue glucose levels as a result of starvation for several days of *Lymnaea stagnalis* (Say, 1821), but glucose levels in the hemolymph remained

constant. Because their experiment tested starvation over several days, and ours examined starvation only up to 12 hr, direct comparisons of the two studies are not possible.

The results of the lettuce analysis suggest that *L. elodes* may obtain some sugars, e.g., glucose, directly from food. Fructose and sucrose were present in lettuce but not in the hemolymph or DG of the snail; maltose, abundantly present in the snail, was not found in lettuce. These results suggest that this snail can convert carbohydrates found in lettuce into the sugars they need for their metabolic processes.

Acknowledgments

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On the Egg Capsules of *Epitonium georgettinum* (Kiener, 1839) (Gastropoda: Epitoniidae) from Patagonian Shallow Waters

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Introduction

The family Epitoniidae is represented in the Patagonian littoral by three known species: *Epitonium magellanicum* (Philippi, 1845); *E. tenuistriatum* (d'Orbigny, 1839); and *E. georgettinum* (Kiener, 1839). The record of *E. albidum* (d'Orbigny, 1842) by Clench & Turner (1951:262) is questionable according to Robertson (1983b). *Epitonium georgettinum* (Kiener) is the only species of Epitoniidae spanning both the Argentinean and Magellanic malacological provinces, from Rio Grande do Sul in Brazil to Puerto Madryn in Argentina (Rios, 1985).

All the species of the family appear to be associated with coelenterates (Robertson, 1983a). *Epitonium georgettinum* is found around the bases of sea anemones that live in intertidal pools and in the adjacent sandy bottom.

The purpose of this note is to describe and illustrate egg masses, capsules, and eggs of *Epitonium georgettinum*. In addition, the life history of the species is compared with that of other species of the genus *Epitonium*.

Materials and Methods

Adult and juvenile specimens and egg masses of *E. georgettinum* were collected from the Patagonian locality of Puerto Pirámide (42°34'S, 64°17'W) in November, 1995 in the Province of Chubut, Argentina (Figure 1). The specimens and egg masses were collected on the sandy bottom with the string of eggs attached to the animals. However, some small specimens were also collected near (less than 4 cm) the pedal disc of sea anemones. The sea anemones (genus *Bunodactis* ?) live on a limestone substrate in the intertidal and infralittoral zones.

The egg masses were housed in the egg collection of the INTECMAR, Universidad Simón Bolívar, Caracas, Venezuela.

Results and Discussion

Egg masses, egg capsules and eggs: The egg masses were found near the adults; in two cases, the female was still spawning, thus carrying the eggs by means of the string. They are composed of 120 to 238 egg capsules

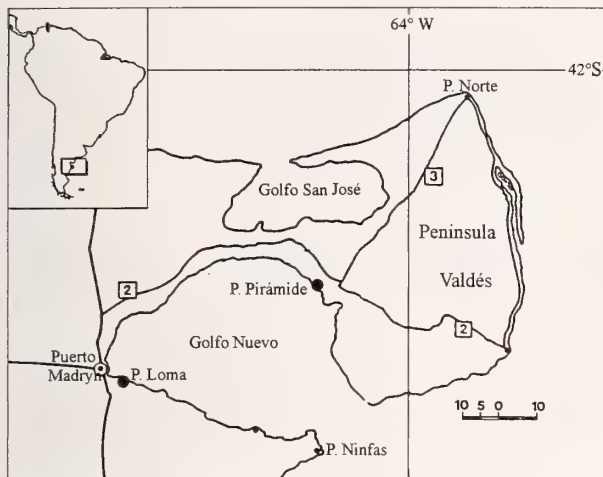


Figure 1

Index map showing the locality where the egg capsules and adults of *Epitonium georgettinum* (Kiener, 1839) were collected.

attached to each other by a tough elastic string (Figure 2). The largest egg capsules recorded measured 1.9×1.5 mm. The egg capsules are pyramidal or polyhedral in shape and covered with sand grains. The number of eggs per capsule ranged from 122 to 211 ($n = 20$; $\bar{x} = 152.55$ $SD = 21.69$). The uncleaved egg is $73\text{--}78$ μm in diameter ($n = 13$ $\bar{x} = 75.15$ $SD = 1.46$). The diameter of the egg is constant, and seems to be independent of the number of eggs per capsule.

The life history of *E. georgettinum* is apparently similar to that of other species of the genus despite differences in the adult size. Some of the live specimens collected reach up to 31 mm in length, which is 10 mm larger than the other Atlantic species of which the life histories are known. The diameter of the uncleaved egg is $73\text{--}78$ μm . It is 68 μm for *E. albidum* (d'Orbigny, 1842) 73 μm for *E. millicostatum* (Pease, 1860), and 78 μm for *E. ulu* Pilsbry, 1921 (see references in Table 1). Larval lifespan and size in *E. ulu* (26 days and 0.39 μm according to Bell, 1985) suggests that *E. georgettinum* spends longer than this as a planktotrophic larva.

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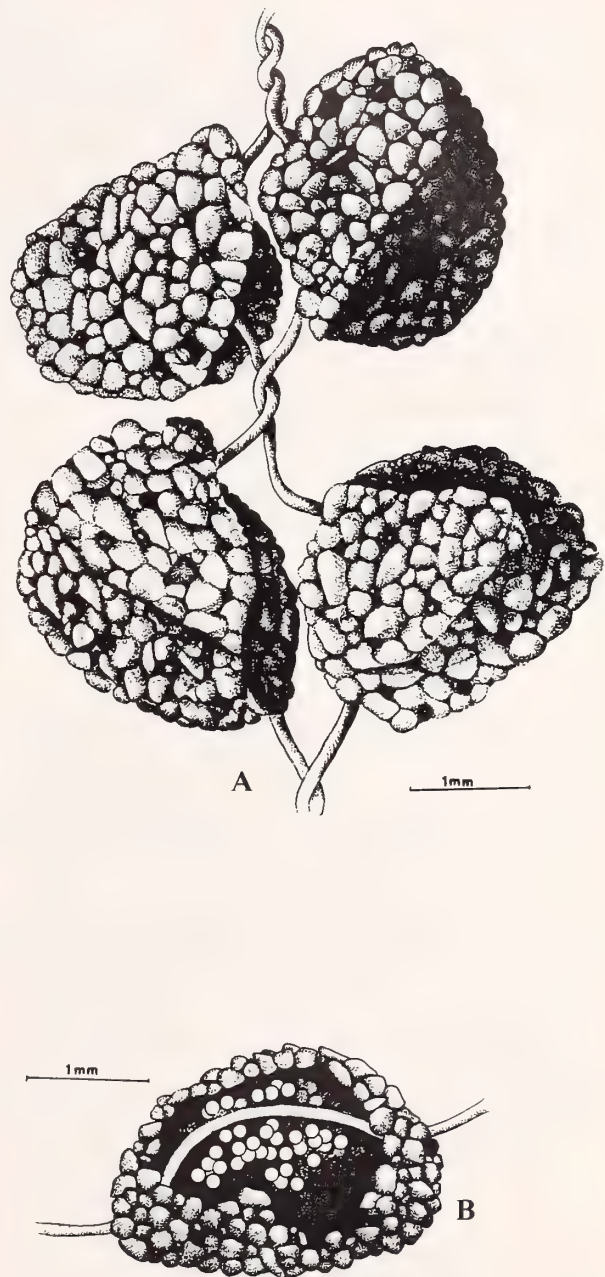


Figure 2

Egg masses of *Epitonium georgettinum* (Kiener, 1839) from Puerto Pirámide, Chubut, Argentina. A. Four egg capsules in life position. B. One broken capsule with the eggs inside.

Table 1

Measurements of number and size of egg capsule and egg in relation with the adult size of *Epitonium* species (in mm unless otherwise indicated).

<i>Epitonium</i> species	Egg capsule size length \times width (or length only)	Egg diameter (μm)	Capsules/egg mass	Eggs/capsule	Adult size (length)	Source
<i>E. millecostatum</i> (Pease, 1860)	1.4 \times 0.87	73	90	149–185 \bar{x} = 165 (n = 3)	9.7	Robertson, 1981
<i>E. equinaticosta</i> (d'Orbigny, 1842)	0.9–1.2	98–106 \bar{x} = 102 (n = 10)	2–11	28–65 \bar{x} = 43 (n = 5)	9.5	Robertson, 1983a
<i>E. albidum</i> (d'Orbigny, 1842)	2.2 \times 0.7	68	2,300	248	8–15	Robertson, 1983b
<i>E. rupicola</i> (Kurtz, 1860)	2.5	?	125	400	19.3	McDennott, 1981
<i>E. ulu</i> Pilsbry, 1921	1.76 \times 1.32	78	?	558	13	Bell, 1985
<i>E. georgettinum</i> (Kiener, 1839)	1.5 \times 1.9	73–78 \bar{x} = 7.51 (n = 13)	120–238	122–211 \bar{x} = 152.5 (n = 20)	31	this paper

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International Commission on Zoological Nomenclature

The following Application was published on 18 December 1998 in Volume 55, Part 4 of the *Bulletin of Zoological Nomenclature*. Comment or advice on this application is invited for publication in the *Bulletin* and should be sent to the Executive Secretary, I.C.Z.N., % The Natural History Museum, Cromwell Road, London SW7 5BD, U.K. (e-mail: iczn@nhm.ac.uk).

Case 3036—*Haliotis clathrata* Reeve, 1846 (non Lichtenstein, 1794) and *H. elegans* Philippi, 1844 (Mollusca, Gastropoda): proposed conservation of the specific names.

Description of a New Species of the Genus *Phidiana* Gray, 1850 (Nudibranchia: Facelinidae) from Pacific Ocean Waters of Panama

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Introduction

In American Pacific waters six species of *Phidiana* Gray, 1850, have been found (Lance, 1962; Bertsch & Ferreira, 1974; Farmer, 1980), although none were reported from the Pacific coast of Panama. During a scientific expedition around some islands belonging to the National Park of Coiba Island, several specimens of a species of *Phidiana* were collected. The color pattern and anatomical features of these specimens allow us to propose a new *Phidiana* species. In this article, the anatomy of the specimens is described and compared with that of other species of the genus.

Materials and Methods

The specimens studied in this article were collected during a scientific expedition in February 1997, around the islands belonging to the National Park of Coiba (Panama), located in the Pacific Ocean. The sample locations

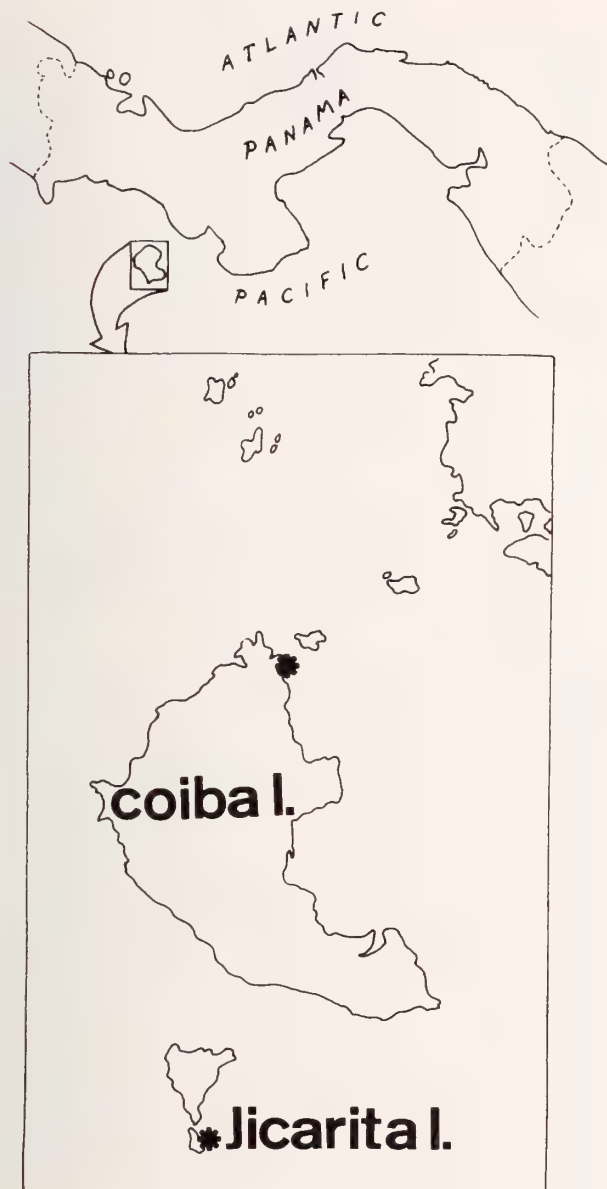


Figure 1

Map of the Coiba islands showing the locations where the specimens were collected (*).

where the specimens were collected are illustrated in Figure 1. The specimens were fixed and preserved in 4% formaldehyde.

Systematic Description

Phidiana mariadelmarae García & Troncoso, sp. nov.
(Figures 2–5)

Type material: Holotype, length 16 mm, collected under rocks in the intertidal zone of Coiba Island, Panama (7

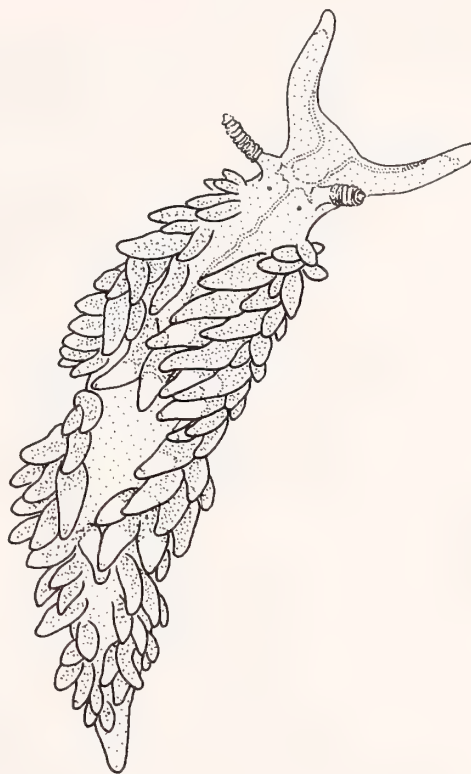


Figure 2

Phidiana mariadelmarae García & Troncoso, sp. nov. External view. The holotype.

February 1997) deposited in Museo Nacional de Ciencias Naturales de Madrid (Spain) with the code number 15.05/27853. Paratype, one specimen of 17 mm in length, collected under rocks in the intertidal zone of Jicarita Island, Panama (9 February 1997) and two specimens (9 and 17 mm in length), collected at the same station (14 February 1997), deposited in the same museum with the code numbers 15.05/27854 and 15.05/30340.

Additional material examined: Two specimens, 9 and



Figure 3

Phidiana mariadelmarae García & Troncoso, sp. nov. A. Jaws. B. Detail of the masticatory border. Specimens 9 and 13 mm.



Figure 4

Phidiana mariadelmarae García & Troncoso, sp. nov. Radular tooth. Specimens 9 and 13 mm.

13 mm in length, collected under rocks in the intertidal zone of Jicarita Island, Panama (9 and 14 February 1997) were dissected.

Etymology: The name of this species, *mariadelmarae*, is derived from the name of the wife and eldest daughter of the first author, María del Mar.

External anatomy (Figure 2): The body is elongated, length was 9, 11, 13, 16 and two of 17 mm, oral tentacles long and cylindrical, rhinophores slightly shorter, and the lower one-third smooth, and two-thirds of the top with 12 annulations. The cerata are two groups of oblique rows, anterior group seven rows, posterior eight rows. Each row has two to seven cerata, the outer shorter than the inner. The genital papilla is on the right side of the body, between the fifth and sixth row of the anterior cerata group. The tail and foot are rounded, propodial tentacles absent.

Coloration. The ground color is orange, slightly darker in the cephalic region. The esophagus, jaws, and subradular membrane are rose colored, as seen through the body wall. The apex of the oral tentacles and apical third of the rhinophores are white. The eyes are clearly visible behind the base of the rhinophores. A fine white longitudinal line extends mid-dorsally from the anterior end of the cardiac region to the level of the rhinophoral base, where it bifurcates. Each branch extends along one side of the head to the apex of the oral tentacle. These lines vary in strength and breakage, depending on the specimen. Thus, in one specimen of 17 mm length, in which the orange coloration of the body is darker than in the other specimens, the white lines are almost absent.

The cerata are hyaline orange. Their orange-brown digestive gland branches are visible through the translucent tissue. The cnidosac color is lighter than the rest of the cerata. On the outer surface of the cerata, located in the cardiac region, there is a white band whose extension on each cerata varies according to specimen. The number of cerata with bands also varies, the most numerous being the specimen that lacks white dorsal lines.

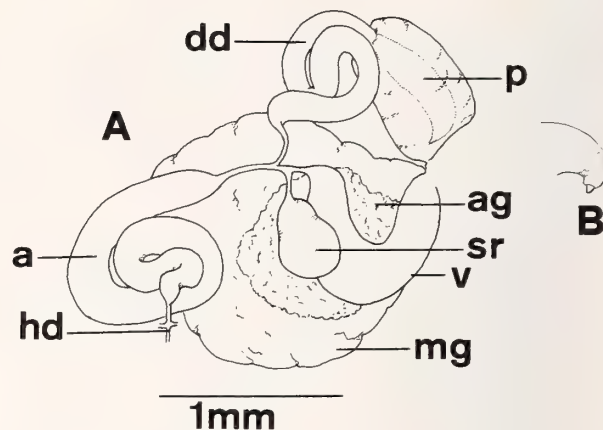


Figure 5

Phidiana mariadelmarae García & Troncoso, sp. nov. **A.** Reproductive system. **B.** Detail of the penis. Abbreviations: a, ampulla; ag, albumen gland; dd, deferent duct; hd, hermaphroditic duct; mg, mucus gland; p, penis; sr, seminal receptacle; v, vagina. Specimens 9 and 13 mm.

Internal anatomy: The jaws (Figure 3) are rose colored, ovate, and strongly convex on the outer surface. The cutting border has a single row with 22 hooked denticles in a specimen of 11 mm in length. The masticatory border of a specimen of 13 mm only has 15 rounded and worn denticles.

The subradular membrane and esophagus are rose colored. The radular formula of a 13 mm long specimen is $20 \times 0.1.0$. The teeth have a large median cusp with three to four hooked denticles on either side, and five hooked lateral cusps. Outer and inner lateral cusps are smaller than median cusps (Figure 4).

The reproductive system is illustrated in Figure 5. The hermaphroditic duct widens into a convoluted ampulla, narrowing at its distal end, bifurcating into a deferent duct and a female duct. The deferent duct enlarges into a long and coiled prostatic duct, similar to the ampulla in length and thickness, which connects with a penis enclosed in a muscular and conical penial papilla. The penis is cylindrical and armed with a curved and pointed apical spine. The common female duct is short and opens into the vaginal vestibule. A short and narrow duct connects the internal end of the vagina with the seminal receptacle.

Discussion

Although the genus *Phidiana* and other related genera have been broadly discussed (Miller, 1974; Gosliner, 1979; Rudman, 1980), our specimens clearly belong to genus *Phidiana*. They have long oral tentacles; the rhinophores are lamellate; the foot is anteriorly rounded; the jaws have a masticatory border with a row of teeth; the radular teeth are provided with lateral denticles on a central cusp; and the penis is ornamented with a spine. Miller

(1974) considered the presence of cerata disposed in parallel rows as a generic characteristic of *Phidiana*. This feature is present in *P. mariadelmarae*.

The coloration of *P. mariadelmarae* differs from that of the majority of *Phidiana* species (Edmunds, 1964; MacFarland, 1966; Rudman, 1980; Willan, 1987). Only *P. lascrucensis* Bertsch & Ferreira, 1974, and *P. pegasus* Willan, 1987, have an orange body color similar to that of *P. mariadelmarae*. However, *P. pegasus* has the rhinophores ornamented by pustules and the foot is enlarged anteriorly with two tentacles, approximately equal in length to the rhinophores (Willan, 1987), whereas in *P. mariadelmarae* the rhinophores are encircled by annulations, and the anterior border of the foot lacks elongated propodial tentacles.

The coloration of *P. mariadelmarae* differs from that of *P. lascrucensis* because this species lacks mid-dorsal longitudinal white lines at the cephalic region, and the dorsal surface of the notum has numerous white spots.

Internally, the radular teeth of *P. mariadelmarae* are similar to those of *P. lascrucensis*. However, they can be differentiated because on the masticatory border of the jaws, *P. lascrucensis* has two rows of denticles, with 23–24 in the first row and five to six in the second. However, *P. mariadelmarae* has only one row with 15–22 denticles. The shape of the denticles differs from other species of *Phidiana*. The denticles in other species are described as rounded or irregular denticles (MacFarland, 1966; Rudman, 1980), whereas in *P. mariadelmarae* they are hooked and pointed.

P. lynceus Bergh, 1867, is an Atlantic species with a mid-dorsal white line bifurcating at the level of the rhinophores as in *P. mariadelmarae*. Both species have a similar reproductive system. However, *P. lynceus* has a line of bright vermilion red that runs from one oral tentacle to the other and the mid-dorsal white line extends from the tail to the rhinophores (Edmunds, 1964).

The reproductive system of *P. mariadelmarae* coin-

cides with that of *P. lascrucensis* since in both species the penis has a curved apex with a spine at the tip. However, because this system was not described in *P. lascrucensis*, is not possible to compare them.

Acknowledgments

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BOOKS, PERIODICALS & PAMPHLETS

Common and Scientific Names of Aquatic Invertebrates from the United States and Canada: Mollusks. Second Edition

by D. D. TURGEON, J. F. QUINN JR., A. E. BOGAN, E. V. COAN, F. G. HOCHBERG JR., W. G. LYONS, P. M. MIKKELSEN, R. J. NEVES, C. F. E. ROPER, G. ROSENBERG, B. ROTH, A. SCHELTEMA, F. G. THOMPSON, M. VECCHIONE & J. D. WILLIAMS. 1998. Common and scientific names of aquatic invertebrates from the United States and Canada: Mollusks. 2nd Edition. American Fisheries Society, Special Publication 26, Bethesda, Maryland. ix + 526 pp. (incl. 16 pls.). ISBN 1-888569-01-8 (paper); ISSN 0097-0638. US\$ 59.00 (includes CD).

In the pages of this journal, informative book reviews typically close with a sentence like “of lasting value to a wide spectrum of readers” or “a fine field companion for work or pleasure on the reefs of the Indo-Pacific.” These concluding sentences typically identify the audience as well as the publication’s value to that audience. As I read this work (hereafter referred to as “the Checklist”), I looked for similar information to incorporate into my final sentence, but unfortunately a clear user group and purpose were not forthcoming. Therefore, I begin my review with what could have been the final sentence: a commendable and Herculean compilation of scientific and common names of northern American mollusks that has yet to identify its larger audience. Moreover, because of the uneven implementation of the principles that were supposed to guide its production, its overall value and usefulness are seriously compromised.

I cannot deny that a handful of colleagues will find this volume a useful source of names for reporting molluscan catch statistics and for legal and regulatory documents. The fact that terrestrial and freshwater taxa are more likely to be mentioned in regulatory documents probably accounts for the better documentation and preparation of these sections compared to the marine groups. However, I doubt that the value of the Checklist will extend to scientific writing or to the professional shell collectors [sic] (p. 13) who the authors claim will welcome the standardization of scientific and common names provided by this volume. Perhaps Riedl (1983:5) expressed it best [translated here from German], “Wanting to collect constant names is the misleading hope of the dilettante; to become aware of the order itself is the rewarded struggle of the expert.”

Much of my conclusion results from my inability to find clear statements as to what the Checklist is supposed to do, and disappointment in how the individual contrib-

utors applied (or failed to apply) the American Fisheries Society’s own principles (pp. 14–16) and the AMU/CSM resolutions (pp. 16–17) to their respective sections. In the final wash, a mixture of rank-driven shuffling, fiat, and phylogenetic tree pruning seems to have controlled much of the production of this chimera.

In the foreword the AFS charge is clear: “*The Committee [on Names of Aquatic Invertebrates] shall be responsible for studying and reporting on matters concerning common and scientific names of aquatic invertebrates and shall prepare checklists of names to achieve uniformity and avoid confusion in nomenclature*” (p. vii). Because the International Code of Zoological Nomenclature (ICZN) already provides oversight to achieve uniformity and avoid confusion in scientific names, I assume that the focus of the AFS charge must be directed primarily at common names. In the Checklist’s introduction, the AFS charge is restated and limited as follows: “Our goal is to keep the scientific nomenclature of this list up to date while achieving uniformity and avoiding confusion in the common names of the mollusks of the United States and Canada” (p. 11). Note that both charges focus only on nomenclature—not systematics, taxonomy, or classification. This is an important distinction and one that is often blurred in our field (and in this Checklist).

The proposal of names and resolution of nomenclatural problems traditionally are dealt with using algorithmic procedures such as the application of the ICZN (B. Roth, personal communication). Algorithms are well suited here because they possess three key features: (1) algorithms are substrate neutral; (2) algorithms consist of small, simple steps; and (3) algorithms have guaranteed results (Dennett, 1995:51). Like the Articles and recommendations of the IZCN, many of the AFS principles and the AMU/CSM resolutions provide algorithmic procedures governing the generation and application of common names.

Until very recently, algorithmic procedures were rarely used in taxonomy. Instead, taxonomy has been strongly dependent on the researcher and his or her wisdom, judgment, and intuition; the results were never guaranteed, even with identical data and training. Recently, the introduction of cladistic methods using explicit assumptions and character analyses has provided workers with an algorithmic procedure to reconstruct phylogenies. If the method, data, and assumptions are identical, it makes no difference whether the algorithms are executed in a laboratory in California or on a veranda in New South Wales. The hypothesis of relationships will be the same.

And most importantly, it can be redone, updated or modified, and repeatedly tested.

Although taxonomy, nomenclature, and even biodiversity itself (see Dennett, 1995) can be viewed as results of algorithmic processes, there is no such validation for the arbitrary assignment of taxonomic ranks or categories to taxa discovered through taxonomic study. Taxonomic ranks are clearly non-algorithmic in their creation and are almost certain to remain so. They are therefore also the most problematic components to apply and justify in systematic studies.

The AFS principles and the AMU/CSM resolutions provided a set of algorithmic procedures for the creation and emendation of the Checklist. Examples include, "No two species on a list shall have the same primary name," "Names shall not violate the tenets of good taste," "Names intended to honor persons . . . are discouraged in that they are without descriptive value," and "The most current literature should be used for systematic classification." In addition to these internal Checklist procedures for common names and the limited classification format, there is also the ICZN for scientific names. We also have a rapidly expanding, recent literature of phylogenetic hypotheses of molluscan relationships available for producing meaningful, phylogenetically based classifications. Unfortunately, in many cases in the Checklist the algorithmic procedures were either not followed or discarded in favor of the old, comfortable "canonical taxonomy" (I thank Barry Roth for coining this very appropriate term; see, for example, *The Veliger* 38:81, 1995). In canonical systematics, authorities make subjective and untestable taxonomic decisions by fiat, which are shoe-horned into rank-driven classifications, and compete in the scientific and popular literature for acceptance. In this brand of systematics, algorithmic procedures are restricted to ICZN nomenclature.

The Checklist sets the stage for its use of canonical systematics early on by setting up phylogenetic systematics as a straw man. In the introduction it is stated that scientific names are "intended" to provide supposed systematic (evolutionary) relationships. This is demonstrably incorrect—historically and even today in many instances. Bartsch, Gould, Pilsbry, Clench, and Keen were all fine taxonomists and together described thousands of taxa. But I do not believe for a minute that they thought they were reconstructing the evolutionary history of groups that they monographed. Keen was explicit about this in her *Sea Shells of Tropical West America* (Keen, 1971); when her former student James H. McLean organized his contributed sections to reflect evolutionary relationships among taxa, and not alphabetically as in the rest of volume, she provided an advisory notice at the beginning of Dr. McLean's section (1971:308). With the exception of W. H. Dall (Lindberg, 1998), few North American malacologists were interested in studying and incorporating evolutionary relationships into their classifications until

the late 1960s and early 1970s. Thus, we are burdened with almost 100 years of canonical taxonomic work that likely reflects little in the way of phylogenetic relationships among taxa. (See Winsor [1995] for the issues surrounding the application of phylogenetic classifications and the history of this debate in England.)

The fallacy that current molluscan classifications are phylogenetically based is clearly exposed in the very next sentence where the authors point out that "... new systematic research and phylogenetic analysis, currently very active areas in malacology, often show that previous ideas of relationships between taxa are wrong and that one or more taxa must be reclassified." Why then should this happen so often? The simplest answer is that most current molluscan classifications are not based on evolutionary relationships. Instead, they were built on overall similarity or on heavily weighted, personal concepts of "good" characters (e.g., radula characters, shell structure, gill morphology). Only in the last 10 years or so has phylogenetic systematics begun to provide alternative hypotheses of relationships. Phylogenetic studies often contradict earlier classifications and can lead to extensive reclassifications of groups. However, the incorporation of published reclassifications of this kind into the Checklist appears to have been uneven.

The plan of the list (p. 12) states that the classification used in the Checklist "approximates" the systematic arrangement of taxa advocated by recent phylogenetic analyses. However, phylogenetic arrangements cannot be pruned and grafted to conform to political and ecological boundaries or popular sensibilities and remain meaningful representations of relationships. Exclusion of taxa that were included in a phylogenetic analysis is likely to produce paraphyletic groupings that confound relationships, and destroy the classification's usefulness in estimating biodiversity and biogeographic distributions—two of the stated goals of the Checklist.

Examples of "approximating the systematic arrangement of taxa advocated by recent phylogenetic analyses" while maintaining traditional groupings include the presence of the "Archaeogastropoda"—a blatantly paraphyletic group that refuses to go away in spite of repeated attacks by both evolutionary systematists and cladists alike (Graham, 1985; Salvini-Plawen & Haszprunar, 1987; Ponder & Lindberg 1997). In the Checklist's incarnation of the "Archaeogastropoda" the Neritopsina are removed from the group, but the taxon Cocculinidae remains grouped within the Archaeogastropoda despite the insightful work of Haszprunar (1988a) and others. While the authors correctly point out that the inclusion of the Cocculinidae within the Neritopsina by Ponder & Lindberg (1997) is not well supported, moving the Cocculinidae to the end of the list of "Archaeogastropoda" to place them next to the Neritopsina does not reflect this uncertainty in this supposedly phylogenetic arrangement of taxa. Because branch segments can freely rotate at

their nodes in a cladogram, it is possible to place the terminal branch label Neogastropoda next to the terminal branch label Patellogastropoda in most gastropod phylogenies. We could then list the taxon names from left to right (or right to left) and have Neogastropoda next to the Patellogastropoda. However, the fact that they are adjacent to one another in no way indicates a close relationship unless they are also sister taxa. These nuances cannot be simply mixed in an amalgamation of traditional canonical systematic practices and phylogenetic classification.

However, the real travesty in the Checklist classification is the absence of the taxon Caenogastropoda. Caenogastropoda was proposed almost 40 years ago by Cox (1960) and subsequently appeared in every meaningful study of gastropod systematics (Bieler, 1991). It is mentioned only once in the Checklist in a footnote to the Gastropoda (p. 56). The absence of the Caenogastropoda from the Checklist seems to hinge on the following statement in the footnote. "Because of the continuing evolution of the higher classification of gastropods, the conflicts between the existing classifications, and the constraints imposed by the nature of this list, we have adopted an arrangement that borrows elements from current classifications and phylogenies while maintaining the utility of and a degree of familiarity with the list for the nonsystematist."

All of these justifications are demonstrably false. Instability in higher gastropod classification? With the exception of the placement of the hydrothermal vent taxa, Neritopsina, and Cocculinidae, the "higher" classification of the Gastropoda has been relatively stable for almost 10 years (Haszprunar, 1988b; Bieler, 1991:table 1; Ponder & Lindberg, 1997). Prior to Haszprunar's (1988b) all-out assault on Thiele's (1925) gastropod classification, Thiele's system was already suspect with the proposal of Neritopsina by Yonge (1947), Cox's (1960) proposal of Caenogastropoda, and Golikov & Scarlato's (1976) classification. Most remaining conflicts are within the larger groupings (i.e., Vetigastropoda, Caenogastropoda), and not questions of monophyly or the relative relationships of the higher taxa used in classification. Constraints imposed by the list? They must have been unwritten for there is nothing in the AFS principles or AMU/CSM resolutions that prevents the use of a modern systematic framework. To the contrary, Resolution 20 states that "*The most current literature should be used for systematic classification,*" and the plan of the list sought to "approximate the systematic arrangement of advocated by recent phylogenetic analyses, *particularly in the gastropods*" (emphasis added). As argued above, there is no algorithm or procedure for combining canonical and phylogenetic classifications, and the results of such mischief do not yield practical or utilitarian classifications. Instead, the "higher gastropod classification" used in the Checklist is unique and is not found in any other systematic

treatment of the gastropods. It therefore cannot be familiar to anyone.

Paradigm changes in science often produce a Tower of Babel effect with different groups of practitioners speaking languages that are unintelligible to one another. The shift from a canonical to a phylogenetic systematics has had such an effect and its residues are acutely apparent in the Checklist. For example, Mikkelsen's (1996) phylogenetic analysis unequivocally supports the demise of the traditional organization of Cephalaspidea. However, her findings are not included in the Checklist because of the "strictures of the organization of this list" (again, the mysterious and secret "list constraints" that are not shared with the reader), and "pending more explicit statements of relationships." Currently, there is no more explicit statement of relationships than the cladogram produced by Mikkelsen's phylogenetic analysis. Perhaps more data or another outgroup might produce a different tree, but it would certainly not be a "more explicit statement of relationships," just a different one. Another confusing rationalization occurs in the footnotes to the Conidae. Here the authors discuss the classification of Taylor et al. (1993), and concede that it "is better supported by anatomical and radular data than any previous one," but then go on to suggest that "... a more 'comfortable' arrangement would have had these four subfamilies in a family of their own."

Personally, I would be comfortable with four elements—air, water, fire, and earth. I can keep all of the them and their elemental and essential qualities in my head, and easily visualize the transformation of water into air by the addition of fire. I cannot keep 112 elements and associated information like atomic number and weights, and electron configuration in my head, nor can I mentally solve the simplest chemical reactions without an aid called the Periodic Table. This table reflects our current and best understanding of the elements, and more importantly allows us to do superior and more predictive science than the Aristotelian elements. Perhaps our classifications have reached the point where ranks and suffixes are no longer sufficient to represent our knowledge, and perhaps we require aids like cladograms and indented listings to represent our best understanding of molluscan classification.¹

One of the most meritorious undertakings of the Checklist framers was the inclusion of Resolution 10—"Justification should be presented when necessary to ex-

¹ This analogy is not as farfetched as it may initially appear. The conception of the Linnaean classification scheme was guided by Linnaeus's belief in a Special Creation, perfection of species, and natural groupings that reflected intelligent design. Phylogenetic classification assumes and seeks to represent descent with modification. The philosophical distance between these two positions is just as great as that between the Aristotelian elements and the Periodic Table.

plain inclusion or deletion of a scientific or common name. (This is a procedural *requirement* [emphasis added] of all editions after the first.)” However, this requirement is too often ignored or shammed throughout the volume. While many of the Checklist authors provided citations to peer-reviewed, primary literature, others used the footnotes to point to seashell trading cards, privately printed and distributed photocopies, and even other checklists to justify nomenclatural choices. According to my copy of the OED a justification is “the action of justifying or showing something to be just, right or proper.” This could be brief, but I assume it would have to contain some explanatory material.

The most blatant lack of justifications for nomenclatural changes is in eastern Pacific bivalves where wholesale changes are referenced to another checklist and therein to another footnote creating a virtual loop of vagueness (see also Resolution 14). For example, in the AFS Checklist (p. 194) *Psephidia stephensae* is considered “to be a synonym of *Nutricula cymata*; *P. stephensae* is deleted.” Checking the supposed justification for this deletion in the cited reference (Coan & Scott, 1997: 25) we find, “We regard *Psephidia stephensae* Hertlein and Grant, 1972, as a synonym of *Nutricula cymata*.” This is a fiat (OED: “an authoritative pronouncement, decree, command, order”) and contains no more information than the action that it supposedly justifies. It remains to be seen whether the long-awaited volume on the marine bivalves of the northeastern Pacific Ocean (Coan & Scott, in preparation) will provide explanations for the multitude of changes made in both checklists. In marked contrast to those who ignored Resolutions 10 and 14, other authors (especially in the terrestrial and freshwater sections) used this resolution to remove and undo unsubstantiated nomenclatural and distributional changes from the first edition.

Other inconsistent applications of the principles and resolutions include the discouraging of patronymics (AFS Principle 6). So while Hemphill lost his slug and Dall, Gould, and Pilsbry their tuskshells, Carpenter kept his carditid, Oldroyd her penshell, and Bartsch his shipworm. There are also some strange biogeographic conventions. Taxa that occur in both the Gulf of Mexico and the tropical eastern Pacific (e.g., *Aplysia parvula*) are listed only as “A” (western Atlantic Ocean including the Gulf of Mexico) because the Pacific Ocean that touches the coast of Mexico is outside the area of coverage of the list. How does one use this list to evaluate biodiversity given this kind of data? There are also logic problems with the exclusion of Hawaiian taxa from the Checklist. One of the reasons Hawaii is excluded from the Checklist is because “its fauna is of Indo-Pacific origin.” Does this mean that the fauna covered in the Checklist must have originated in the US and Canada with the exception of the introduced taxa in Appendix 4? Absolutely not: Marinovich (1983), Vermeij et al. (1990), Lindberg (1991), McLean

(1984), and others have convincingly demonstrated biotic interchange between North America and the temperate regions of Asia and South America. There is also substantial overlap of the Arctic fauna (which is covered in the Checklist) with the faunas of Greenland, Iceland, and Arctic Europe. Was it assumed that widely dispersed Arctic taxa originated in North America and subsequently migrated out of the New World?

While the AFS charge was clear, the authors’ goals laudable, and the principles and resolutions unambiguous and comprehensible, the 2nd edition of “Mollusks” does not overcome the past and, regrettably, some of the present practices of molluscan taxonomy. The appendices of endangered and threatened mollusks, extinct mollusks, and introduced mollusks are useful and welcome additions, but the remaining three appendices (“For readers who are relatively new to the field of malacology, . . .”) seem out of place and passé. They also provide little information for the neophyte. For example, the illustration of chiton anatomy in the appendix “Introduction to North American Mollusks” shows only a mouth, anus and gills in addition to the requisite plates and girdle. Evidently, these animals do not reproduce or have other life functions. Anatomical illustrations of bivalves, scaphopods, gastropods, and cephalopods show those taxa to be better endowed, but not so the aplacophorans. The coiled monoplacophoran protoconch, debunked by Lindberg (1985) and Wingstrand (1985) makes a return appearance in this appendix as well. The Checklist’s introductory materials and many of the appendices are almost identical to the introductory material of the first edition of *American Seashells* (Abbott, 1954)—*Man and Mollusks*, *Life of [Mollusks]*, *Collecting North American Mollusks*, *Guide to the Molluscan Literature*. It’s all there; even the dedication to the esteemed author of two editions of *American Seashells*—R. Tucker Abbott.

What about the 3rd edition of the Checklist? A limited view of the future is on the CD that accompanies the Checklist volume. Adobe Acrobat® Reader 3.0.1 is supplied on the disc and with it the user can display on-screen facsimiles of the Checklist. The display is in the form of several related documents and each document is searchable. Ten years from now it is unlikely that hard copy of the 3rd edition of the Checklist will need to be produced. The future most likely contains distributed taxonomic resources, where individual researchers maintain their most recent monographic treatments, data, and classifications on the World Wide Web (or whatever the web becomes). Rather than open a book, we will likely send our electronic assistants to the Checklist URL (e.g., www.IBM.checklist.org) to access a meta-database of distributed taxonomic resources that will then be queried and the results (and supporting data) returned to you in the blink of an eye. For those who cannot wait 10 years, the book/CD combination is available from AFS Publi-

cation Fulfillment, P.O. Box 1020, Sewickley, PA 15143 USA.

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Taxonomic Atlas of the Benthic Fauna of the Santa Maria Basin and Western Santa Barbara Channel. Volume 8.

The Mollusca Part 1—The Aplacophora, Polyplacophora, Scaphopoda, Bivalvia and Cephalopoda

edited by P. VALENTICH SCOTT & J. A. BLAKE. 1998. Santa Barbara Museum of Natural History, Santa Barbara, California. viii + 250 pp. ISBN 0-936494-13-1.

"The Mollusca Part 1" of the *Taxonomic Atlas* contains treatments of the Aplacophora by Amélie H. Scheltema, the Polyplacophora by Douglas J. Eernisse, the Scaphopoda by Ronald L. Shimek, the Bivalvia by Paul Valentich Scott, and the Cephalopoda by F. G. Hochberg; there is a brief general introduction to the Mollusca by Eugene V. Coan. This work completes coverage of the phylum along with the earlier-published Part 2, the Gastropoda by James H. McLean and Terrance M. Gosliner (reviewed in *Veliger* vol. 39, no. 3). The specimen material described is mainly that collected during U.S. Department of the Interior Minerals Management Service (MMS) benthic monitoring in the Santa Maria Basin off central California, from about Point Estero to Point Conception, and the western Santa Barbara Channel, south-east of Point Conception, in depths of approximately 100–600 m.

The relevance of the work, however, extends beyond those geographic limits; and each individual contribution

includes general information about its taxonomic group and advice on collection, preservation, and laboratory methods applicable to the taxon as a whole. An appendix with maps and station lists relates to all articles; except for this, and a general index, each section is in effect free-standing, with its own bibliography and self-contained illustrations. The quality of the figures, both line drawings and photographs, ranges from good to superb. Dealing as they do with disparate clades of organisms, the articles differ among themselves as to the characters and the detail they address. All, however, are pragmatically oriented and helpful to potential users—the way a taxonomic atlas should be.

Five new species and one monotypic new species are described by Scheltema in the Aplacophora, and two new species by Valentich Scott in the Bivalvia. Several new taxonomic combinations occur, of which *Enteroctopus dofleini* (Wülker, 1910) for the Giant North Pacific Octopus will perhaps attract the most notice.

The volume and series are available from the Department of Invertebrates, Santa Barbara Museum of Natural History, 2559 Puesta Del Sol Road, Santa Barbara, California 93105-2936, U.S.A.

B. Roth

Land Snails of New Mexico

edited by A. L. METCALF and R. A. SMARTT. 1997. Bulletin 10, New Mexico Museum of Natural History and Science. iii + 145 pp.

This work consists of three related papers. The first, "Land snails of New Mexico: a systematic review" (pp. 1–69) by Metcalf and Smartt, surveys snail and slug species occurring in the state, emphasizing present geographic, altitudinal, and habitat distribution. "Land snails of New Mexico from a historical zoogeographic point of view" (pp. 71–108) by Metcalf discusses and evaluates efforts to delineate zoogeographic provinces for the land snails in southwestern United States, describes geologic events and fossil faunas of the region from later Mesozoic to Quaternary time, and proposes a model of Cenozoic historical geography of the New Mexico terrestrial mollusk fauna. "Altitudinal distributions of land snails in some montane canyons in New Mexico" (pp. 109–127) by Timothy J. Dillon and Metcalf focuses in on the results of collecting along six transects in New Mexico mountain ranges. Two appendices present the underlying data on taxa and localities for the first and third articles.

The work is available from the New Mexico Museum of Natural History and Science, 1801 Mountain Road NW, Albuquerque, NM 87104 U.S.A.

B. Roth

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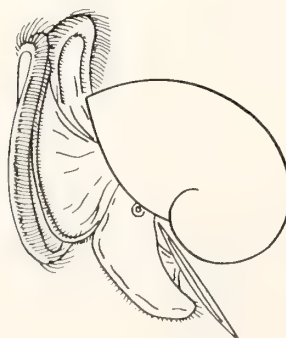
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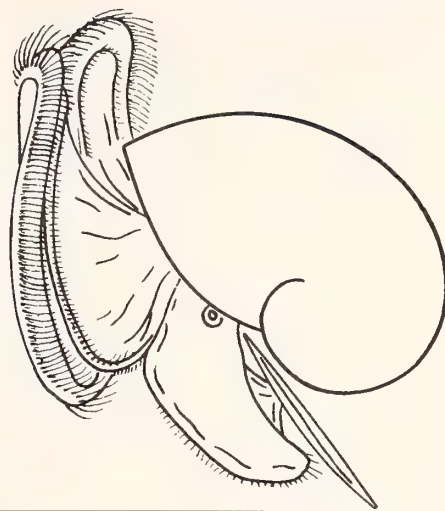
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THE VELIGER

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A New Species of *Doriopsilla* (Nudibranchia: Dendrodorididae) from the Pacific Coast of North America, Including a Comparison with *Doriopsilla albopunctata* (Cooper, 1863)

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Abstract. Much confusion has surrounded the systematics of the yellow species of Dendrodorididae inhabiting the Pacific coast of North America. Re-examination of *Doris albopunctata* Cooper, 1863, indicates that it is properly placed in *Doriopsilla*. Examination of specimens from different localities throughout California, the Pacific coast of Baja California, and within the Gulf of California, indicates that all white-gilled specimens are conspecific with *D. albopunctata*, and that *D. fulva* (MacFarland, 1905) and *D. reticulata* (Cockerell & Eliot, 1905) are regarded as junior synonyms. A second species with yellow gills is here described as *Doriopsilla gemela*. It differs from *D. albopunctata* in aspects of its color pattern, external morphology, digestive system, reproductive anatomy, and developmental biology. The two species also differ in allozyme allelic frequencies. *Doriopsilla gemela* and *D. albopunctata* are also compared to other members of the genus present in the eastern Pacific. These comparisons show that, while *D. gemela* and *D. albopunctata* are externally similar to each other, their internal anatomy is more similar to other species than to each other.

INTRODUCTION

Much confusion has surrounded the systematic status of yellow porostomate dorids on the Pacific coast of North America. Cooper (1863) described *Doris albopunctata* from Santa Barbara, California. MacFarland (1905) later described *Doriopsis fulva* from Monterey Bay, California, and Cockerell & Eliot (1905) described *Doridopsis reticulata* from San Pedro, California. Steinberg (1961), Roller (1970), McDonald (1983), and Valdés & Ortea (1997) considered these three species as synonymous. Behrens (1980, 1991) considered *Dendrodoris fulva* as distinct from *Doriopsilla albopunctata*. Behrens (1980, 1991), McDonald & Nybakken (1980), and McDonald (1983) considered another species (as *Dendrodoris* sp. 1 and *Dendrodoris* sp. A, respectively) with yellow rather than white gills and different egg ribbon shape as a distinct, undescribed species. Despite the above differences, no detailed examination of anatomy, developmental biology, or genetic differences has been undertaken. This paper

examines these taxa in detail to determine systematic relationships.

MATERIALS AND METHODS

In order to study the anatomy, developmental biology, and genetic variability of the two species of *Doriopsilla*, numerous specimens of both species were collected and examined. Specimens for anatomical study were collected from five localities along the central and southern California coast and from several localities on both coasts of Baja California. More than 15 individuals of each species were examined to ascertain intraspecific and interspecific anatomical variability.

For developmental studies, live specimens of *Doriopsilla albopunctata* were collected from five localities along the central and southern California coast. Specimens of *D. gemela* were collected from Hill Street, San Diego. Specimens were maintained in the seawater system at San Francisco State University and at the Steinhart Aquarium of the California Academy of Sciences.

Allozyme samples were conducted on 54 nudibranchs. Of these individuals 12 were *Doriopsilla gemela* from Hill Street. Forty-two individuals of *D. albopunctata* were sampled for allozyme comparison, including 12 specimens from Hill Street, San Diego, eight from Bird Rock, San Diego, eight from Diablo Canyon, San Luis Obispo County, 11 from Carmel Point, Monterey County, and three from Pillar Point, San Mateo County. Specimens were dissected. The anterior half of each animal was fixed in Bouin's fixative for anatomical comparison as vouchers. The posterior portions of the fresh tissue samples were homogenized in 1:1 volume ratio of tissue to homogenizing buffer. All samples were blotted on Whatman #2 filter paper. Excess moisture was wiped off of samples, and samples were placed in horizontal 11% starch gels. Gels were cooled by placing Blue Ice packs on top of the running gel. Two gel conditions were run at 150 volts on Heathkit model IP-17 power supplies. One gel system was Poulik's discontinuous buffer (electrode buffer pH 8.2, gel buffer pH 8.7), and was run for 5 hours. The other gel system was an amine citrate continuous buffer system at pH 7.8, and was run for 3.5 hours. Staining of the gels was undertaken by standard procedures. Ten allozyme stains were attempted. The allozymes attempted on the Poulik's gel were Superoxide dismutase (S.O.D.), Tri-Peptidase-1 and -2 (Trip-1, Trip-2), Phosphoglucose Isomerase (P.G.I.), Mannose Phosphate Isomerase (M.P.I.), and Phosphoglucomutase (P.G.M.). The allozymes attempted on the Amine-citrate gel were Superoxide dismutase (S.O.D.), Creatin Kinase (C.K.), Adenalin Kinase (A.K.), Malate Dehydrogenase (M.D.H.), Isocitrate dehydrogenase (I.D.H.), and 6 Phosphogluconic Acid Dehydrogenase (6P.G.D.H.). These allozymes were chosen because they have a high success rate of staining in a broad array of animal species, and several overlapped with those used in previous nudibranch allozyme investigations (Havenhand et al., 1986 and Morrow et al., 1992). The six allozymes which were scored under these gel conditions were Superoxide Dismutase, Tri-Peptidase 1 and 2, Malate Dehydrogenase, Phosphoglucose Isomerase, and Phosphoglucomutase.

SPECIES DESCRIPTIONS

Doriopsilla albopunctata (Cooper, 1863) (Figures 1A,B, 2A,D, 3A,B, 4A)

Doris albopunctata Cooper 1863: 58.

Doriopsis reticulata Cockerell in Cockerell & Eliot, 1905: 41-42, pl. 7, fig. 5.

Doriopsis fulva MacFarland, 1905: 45.

(see McDonald, 1983 for complete synonymy)

Distribution: Known from Puerto Peñasco and Bahía de los Angeles, Gulf of California, México; Bahía Tortugas, Baja California Sur, México to Van Damme State Beach, Mendocino County, California (Marcus & Marcus, 1967; Behrens, 1991; present study).

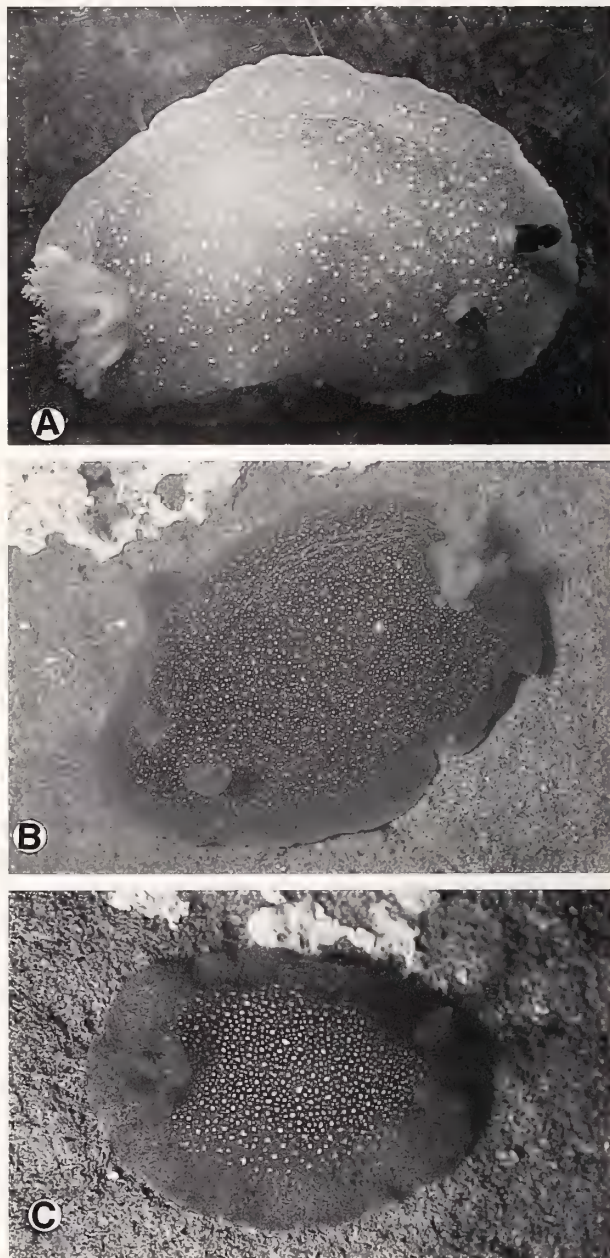


Figure 1

Living animals. A. *Doriopsilla albopunctata* (Cooper, 1863), specimen from Monterey, California showing low dorsal spot density. B. *Doriopsilla albopunctata* (Cooper, 1863), specimen from San Diego, California, showing high dorsal spot density. C. *Doriopsilla gemela* Gosliner, Schaefer & Millen, sp. nov., specimen from San Diego, California.

Material examined: One specimen, dissected, CASIZ 111388, intertidal zone, Carmel Point, Monterey County, California, 29 July 1996, M. Schaefer, coll.. One specimen, dissected, CASIZ 111389, intertidal zone, Pillar Point, San Mateo County, California, 3 June 1996, T.

Gosliner, coll. One specimen, dissected, CASIZ 111390, Hill Street, San Diego, California, 1 August 1996, M. Schaefer, coll. One specimen, dissected, CASIZ 111391, Punta Gringa, Bahía de los Angeles, Baja California, México, March 1997, H. Bertsch, coll. One specimen, dissected, CASIZ 112215, Punta Gringa, Bahía de los Angeles, Baja California, México, March 1997, H. Bertsch, coll. Two specimens dissected, intertidal zone, Pacific Grove, Monterey County, California, June 1976, S. Millen, coll. Two specimens dissected, 23–27 m depth, Scripps Canyon, La Jolla, California, 1 September 1996, M. Miller, coll. Two specimens, CASIZ 071498, intertidal zone, Centro de Acuicultura, Bahía Tortugas, Baja California Sur, México, 29 June 1984, T. Gosliner, coll. Six specimens, one dissected, CASIZ 072134, 20–23 m depth, Roca Ben, Baja California, México, 20 August 1987, R. Van Syoc, T. Gosliner, coll.

External morphology: The living animals (Figure 1A,B) reach a maximum of 60 mm in length. The body color ranges from bright yellow, orange to chestnut brown. The dorsal surface is ornamented with opaque white spots, some of which are present in the center of conical tubercles. The tubercles are 0.6–1.0 mm in diameter. The spots in the center of the tubercles are small glands, which are bordered by spicules. The size and density of tubercles varies greatly, within and between localities. Specimens from northern California are usually bright yellow throughout, but may occasionally have a central patch of chestnut brown on the dorsum. Specimens from southern California exhibit much more variation in color than do northern California specimens, but are generally much darker in color. The rhinophores are orange-yellow to yellow, with 11–30 lamellae. There are five to six bi- or tripinnate gills which are white to pale yellow in color. The notum is densely spiculate. The foot is elongate, but is generally completely covered by the posterior end of the mantle. The head is poorly developed with minute ridges.

Internal morphology: The oral tube (the presumed homolog of the buccal mass in other dorids that possess a radula) lacks any vestige of a radula. It (Figure 2A) is elongate and tubular and can be wider posteriorly when the tube is not fully extended. It passes through the anterior nerve ring, and forms a junction with the esophagus. Posteriorly, the esophagus is narrower than the oral tube and is uniformly cylindrical and glandular. From the junction of the oral tube and the esophagus, immediately anterior to the nerve ring, a pair of muscles emerges and joins the nerve ring. A second pair of muscles attaches to the base of the buccal ganglia and traverses the length of the glandular portion of the esophagus and joins the muscular portion of the esophagus (gizzard of Marcus & Marcus, 1967). These muscles function as retractor muscles for the oral tube. Posterior to the short muscular section of the esophagus is another glandular segment which

enters the stomach within the bilobed, highly digitate digestive gland. At the junction of the short muscular portion of the esophagus and this glandular segment, a second pair of retractor muscles emerges and connects posteriorly with connective tissue near the gills. The intestine emerges between the two lobes of the digestive gland. Here the widest portion of the intestine has several laterally directed glandular lobes. At this point, a short rounded pyloric caecum extends from the intestine, where it is situated ventrally. The intestine narrows and continues posteriorly to the anus, which is situated to the far left side, between the left lateral branchial plumes.

The reproductive system (Figure 2D) is triaulic. A short preampullary duct widens into an elongate, cylindrical ampulla. The ampulla divides into a short oviduct, which enters the female gland mass and the more elongate vas deferens. The proximal portion of the vas deferens expands into a wide, flattened, lobed prostatic portion which envelops most of the bursa copulatrix. From the distal end of the prostatic portion, the vas deferens narrows abruptly, then gradually widens and curves into the penial bulb. The penial bulb lacks a distinct penial papilla and contains approximately 16 rows of curved, acutely pointed penial hooks which are approximately 25–35 μm wide at the base and up to 50 μm in length (Figure 3A,B). The vaginal opening, like the penial bulb, is also narrow. The vagina is relatively narrow and straight. At its proximal end is a large, thin-walled, spherical bursa copulatrix. The slender receptaculum seminis is extremely elongate and extends beyond the proximal end of the bursa copulatrix. The duct of the receptaculum seminis joins the vagina proximally, near the base of the bursa copulatrix. Near this junction, the uterine duct emerges and joins the female gland mass. The female gland mass is large and completely developed in all specimens examined.

Developmental biology: Egg ribbons (Figure 4A) are in the form of a long, narrow, spiral ribbon attached on one edge, consisting of one to three whorls. The ribbon is crenulate along its free edge and may be 2–4 mm in height. This ribbon shape is classified as type A (Todd, 1983). Egg laying in Monterey Bay occurs throughout the year, with an increase in the summer months (MacFarland, 1906). The ribbon size, height, and number of whorls are variable, and are dependent on the size of the adult which produced it. Egg ribbon color can be yellow, orange, or off-white. These ribbons almost always have a single egg per capsule. The occurrence of two larvae per egg is rare. Capsules vary from 180 to 240 μm across, with larvae initially measuring 100–150 μm across. Planktotrophic larvae with type B shells (Todd, 1981), previously known as type 1 (Thompson, 1961) hatch after 31 days at 14°C.

Genetic variation: To ascertain genetic variability within and between populations of *Doriopsilla albopunctata*, 12

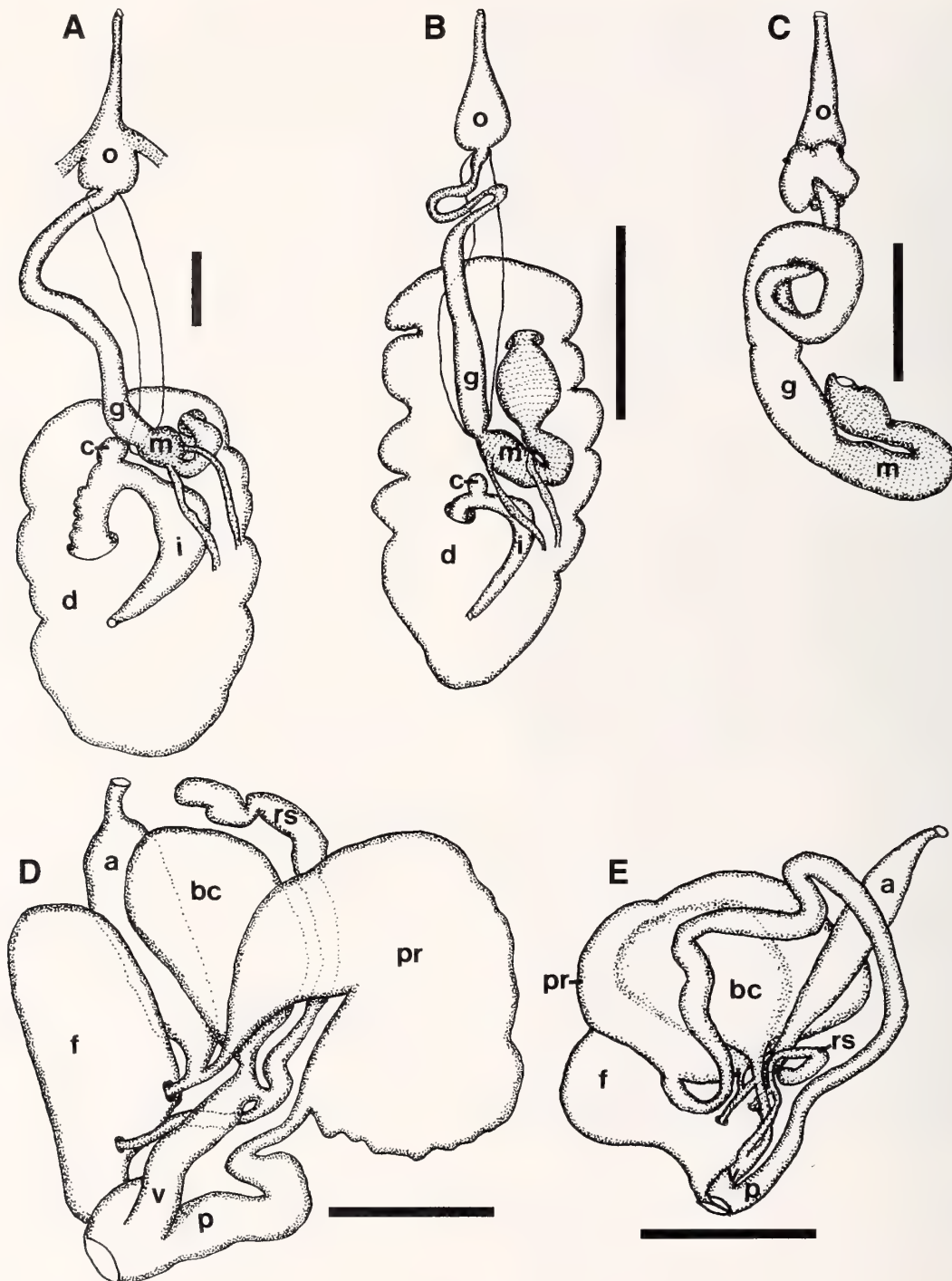


Figure 2

A, *Doriopsilla albopunctata* (Cooper, 1863), oral tube and esophagus of specimen from Bahía de los Angeles (CASIZ 112215), with blood gland and central nervous system removed, c = caecum; d = digestive gland; g = glandular portion of esophagus; i = intestine; m = muscular portion of esophagus; o = oral tube, scale = 3 mm.
 B, *Doriopsilla gemela* Gosliner, Schaefer & Millen, sp. nov., oral tube and esophagus of specimen from Bahía Tortugas (CASIZ 071505), with blood gland and central nervous system removed, c = caecum; d = digestive gland; g = glandular portion of esophagus; i = intestine; m = muscular portion of esophagus; o = oral tube, scale

individuals from Hill Street, San Diego County were compared with 11 individuals from Carmel Point, Monterey County; the two localities are 685 km apart. Six loci were examined for allozymatic variation (Schaefer, in preparation). The genetic identity measure, *I* (Nei, 1972), within this species for the two different populations is 0.950, using allozyme comparisons. The *I* value ranges from 1 (if the populations are identical) to 0 (no common alleles). Conspecific populations have *I* values above 0.9 among varied plants and animals (Thorpe, 1983; Nei, 1987). The genetic distance, *D* (Nei, 1972), was 0.052 between the two populations. Values for *D* vary from 0 (if the populations are identical) to infinity (no common alleles). Allelic frequencies at both sites were within expected parameters as to indicate Hardy-Weinberg Equilibrium, as determined by chi square analysis.

Doriopsilla gemela Gosliner, Schaefer & Millen,
sp. nov.

(Figures 1C, 2B,C,E, 3C–E, 4B)

yellow-gilled porostome Behrens, 1980:102, fig. 146.

Dendrodoris sp. A McDonald & Nybakken, 1980:54–55, fig. 57; McDonald, 1983:171.

Dendrodoris sp. 1 Behrens, 1991:71, fig. 130.

Distribution: Known from the Gulf of California, México, from Bahía de los Angeles and along the Pacific coast of North America from Bahía Tortugas, Baja California Sur, México to Elkhorn Slough, Monterey County, California (Behrens, 1991; present study).

Etymology: The name *gemela* comes from the Spanish for twin, as this species is externally similar to its sympatric congener *Doriopsilla albopunctata*.

Type material examined: Holotype, CASIZ 111392, intertidal zone, Hill Street, San Diego, California, 1 August 1996, M. Schaefer, coll. Paratypes: One specimen, CASIZ 111393, same locality, date, and collector as holotype. One specimen, CASIZ 111394, same locality, date, and collector as holotype. One specimen, dissected, CASIZ 111395, same locality, date, and collector as holotype. Fifteen specimens, one dissected, CASIZ 071505, intertidal zone, Centro de Acuacultura, Bahía Tortugas, Baja California Sur, México, 29 June 1984, T. Gosliner, et al., coll. Three specimens, one dissected, CASIZ 074648, in-

tertidal zone, Centro de Acuacultura, Bahía Tortugas, Baja California Sur, México, 28 June 1984, S. Klontz, D. Catania, and R. Van Syoc, coll. One specimen, CASIZ 074649, 3–5 m depth, Los Morros, mouth of Bahía Tortugas, Baja California Sur, México, 1 July 1984, T. Gosliner, coll. One specimen, CASIZ 074647, intertidal zone, Centro de Acuacultura, Bahía Tortugas, Baja California Sur, México, 1 July 1984, T. Gosliner, coll. One specimen, CASIZ 073523, 7 m. depth, Punta Gringa, Bahía de los Angeles, Baja California México, 20 September 1991, T. Gosliner, coll. Seven specimens, two dissected, CASIZ 074642, intertidal zone, Centro de Acuacultura, Bahía Tortugas, Baja California Sur, México, 2 July 1984, H. Bertsch, coll. One specimen, CASIZ, 071661, 9 m. depth, Punta Gringa, Bahía de los Angeles, Baja California México, 30 June 1987, S. Millen, coll.

External morphology: The living animals (Figure 1C) reach a maximum of 40 mm in length. The body color is bright yellow to orange or orange-brown. The dorsal surface appears smooth but has some minute tubercles, 0.20–0.24 mm in diameter. The notum is ornamented with small opaque white spots. The rhinophores are orange-yellow to yellow, with 7–10 lamellae. There are five to seven bi- or tripinnate gills, which are bright yellow to orange in color. The notum is densely spiculate. The foot is elongate, but is generally completely covered by the posterior end of the mantle. The head is poorly developed with triangular, furrowed tentacles.

Internal morphology: The buccal mass lacks any vestige of a radula. The oral tube (Figure 2B, C) is elongate and tubular. It is widest posteriorly at its junction with the narrow, glandular esophagus. The esophagus narrows at the point where it passes through the anterior nerve ring. Posteriorly it is cylindrical, and widens gradually forming one or more loops. The granular surface appears to contain glandular cells. Posterior to the elongate glandular segment is an elongate, curved muscular portion of the esophagus, which widens into a short, rounded glandular section immediately anterior to where it joins the stomach within the bilobed digestive gland. The two lobes of the digestive gland are well separated from each other, and their outer edges are partially subdivided by vertical partitions in the body wall. The intestine emerges between the two lobes of the digestive gland. At this point a short rounded pyloric caecum extends dorsally from the intes-

←

= 2 mm. C. *Doriopsilla gemela* Gosliner, Schaefer & Millen, sp. nov., oral tube and esophagus of specimen from Hill Street, San Diego (CASIZ 111395) with blood gland removed g = glandular m = muscular portion of esophagus; o = oral tube, scale = 1 mm. D. *Doriopsilla albopunctata* (Cooper, 1863), reproductive system of specimen from Pillar Pt. (CASIZ 111389), a = ampulla; bc = bursa copulatrix; f = female gland mass; p = penis; pr = prostate; rs = receptaculum seminis; v = vagina, scale = 2 mm. E. *Doriopsilla gemela* Gosliner, Schaefer & Millen, sp. nov., reproductive system of specimen from Hill Street, San Diego (CASIZ 111395), a = ampulla; bc = bursa copulatrix; f = female gland mass; p = penis; pr = prostate; rs = receptaculum seminis; v = vagina, scale = 1 mm.

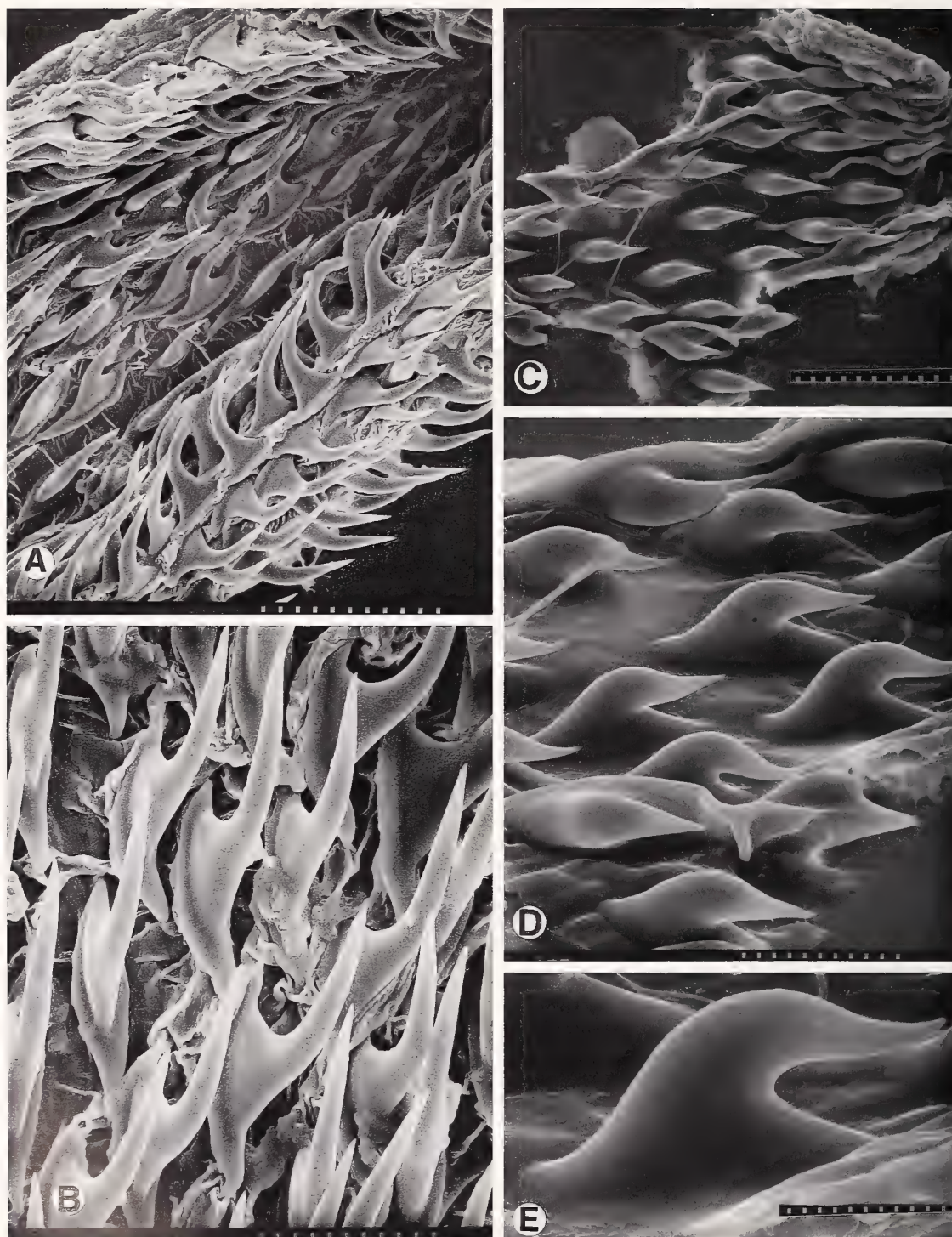


Figure 3

Penial spines. A. *Doriopsilla albopunctata* (Cooper, 1863), from Pillar Point, San Mateo County, (CASIZ, 111389), showing entire width of vas deferens, scale = 75 μ m. B. *Doriopsilla albopunctata* (Cooper, 1863), isolated spines, scale = 30 μ m. C. *Doriopsilla gemela* Gosliner, Schaefer & Millen, sp. nov., from Bahía Tortugas (CASIZ 071505), entire width of vas deferens, scale = 30 μ m. D. *Doriopsilla gemela* Gosliner, Schaefer & Millen sp. nov., from Bahía Tortugas (CASIZ 071505), vas deferens, scale = 15 μ m. E. *Doriopsilla gemela* Gosliner, Schaefer & Millen, sp. nov., from Bahía Tortugas (CASIZ 071505), isolated penial spine, scale = 7.5 μ m.

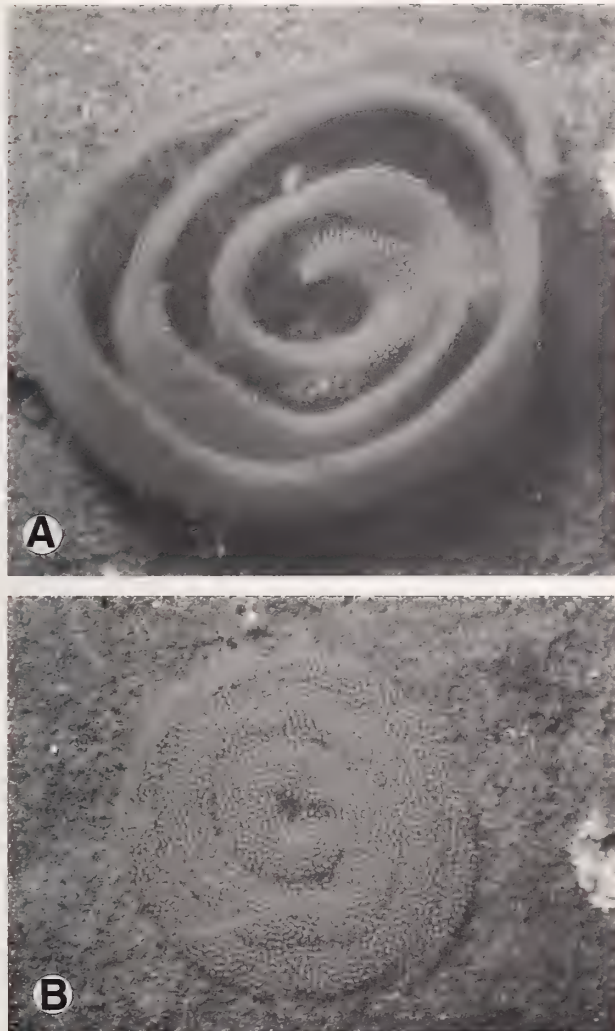


Figure 4

Egg masses. A. *Doriopsilla albopunctata* (Cooper, 1863), from Carmel Point, California. B. *Doriopsilla gemela* Gosliner, Schaefer & Millen, sp. nov., from Hill Street, San Diego, California.

tine. The intestine narrows and continues posteriorly to the anus, which is on the left side, situated between the left lateral branchial plumes.

The reproductive system (Figure 2E) is triaulic. A short preampullary duct widens into an elongate, cylindrical ampulla. The ampulla divides into a short oviduct, which enters the female gland mass and the more elongate vas deferens. The proximal portion of the vas deferens widens into a wide, highly digitate, flattened prostatic portion, which envelops most of the bursa copulatrix. From the distal end of the prostatic portion the vas deferens narrows abruptly into the elongate, convoluted ejaculatory portion which is highly muscular. The ejaculatory portion of the vas deferens remains relatively narrow throughout its length and does not widen at the penial bulb, which

is relatively short. The penis contains approximately six rows of curved, acutely pointed penial hooks which are approximately 10–15 μm wide at the base and 15–20 μm in length (Figure 3C–E). The vaginal opening is enlarged and muscular. The vagina is relatively narrow and straight. At its proximal end is a large, thin-walled, spherical bursa copulatrix. The slender receptaculum seminis is extremely elongate and curved. The duct of the receptaculum seminis joins the vagina distally, near the base of the vaginal duct. From the middle of the receptaculum duct, the uterine duct emerges and joins the female gland mass. The female gland mass is large and completely developed in all specimens examined.

Developmental biology: Egg ribbons (Figure 4B) are flat, transparent spirals consisting of three whorls and containing yellow eggs. A 15 mm adult produced an 8 mm ribbon with 2000 eggs. Each capsule has one egg, 240 μm wide. The larvae initially almost fill this capsule. Eggs can vary from 120 to 300 μm wide. The occurrence of two larvae per egg is rare. Lecithotrophic larvae hatch after 31 days at 14°C, with type B shell shape (Todd, 1981) previously known as type 1 (Thompson, 1961). Some species of opisthobranchs exhibit poecilogony and can change their developmental strategy from lecithotrophic larvae or direct development to planktotrophic larvae in response to adult starvation or other environmental variation (Clark & Goetzfried, 1978). Animals from the Hill Street population were subjected to starvation but did not demonstrate any change in reproductive strategy.

Population genetics: The genetic identity measure, *I* was 0.374 between the species *Doriopsilla albopunctata* and *Doriopsilla gemela*. Both species were collected from Hill Street, San Diego County for the interspecific allozyme comparison. Typically, populations of congeneric species have *I* values from 0.3 to 0.8 (Thorpe, 1983; Nei, 1987). The genetic distance value, *D*, was 0.983 between these two species. Allelic frequencies were within expected parameters as to indicate Hardy-Weinberg Equilibrium, as determined by chi square analysis, with the exception of MDH, which occurred as three homozygotic alleles with no detected heterozygotes. This is significant at the 0.005 level, as determined by chi square analysis. Details of methodology and banding patterns are presented by Schaefer (in preparation).

DISCUSSION

The systematics of the genera within the Dendrodorididae has been historically the subject of considerable confusion. The names *Dendrodoris* Ehrenberg, 1831, *Doriopsis* Pease, 1860, *Doridopsis* Alder & Hancock, 1864, and *Doriopsilla* Bergh, 1880, have been applied to various members of the family. Pruvot-Fol (1930) showed that *Doridopsis* is a junior synonym of *Dendrodoris*, but con-

sidered *Doriopsis* to be a member of the Archidorididae. Subsequently, *Doriopsis* has been placed in the Dorididae (Kay & Young, 1969). Regardless of its familial placement, *Doriopsis* has a well-developed radula and pectinate gills and is clearly not a dendrodorid.

Eliot (1906) recognized the distinction between *Dendrodoris* (as *Doridopsis*) and *Doriopsilla*, with the former having elongate buccal nerves and more posteriorly situated buccal ganglia. Valdés & Ortea (1997:240) questioned this distinction and stated that Eliot was incorrect in stating that the buccal ganglia in *Doriopsilla* were situated anteriorly. However, they did not describe or illustrate the position of the buccal ganglia of any of the species they described. The differences in buccal ganglion position noted by Eliot has been confirmed by other authors. Marcus (1957:fig.) and Edmunds (1971:figs. 21d, 22d) have shown the more posterior position of the ganglia in several species of *Dendrodoris*. Several other authors (Marcus, 1961:fig. 19; Marcus & Marcus, 1967:fig. 62; Gosliner, 1991:fig. 8) have indicated that the position of the buccal ganglia in species of *Doriopsilla* is within the anterior nerve ring. The two species of *Doriopsilla* examined here also have the buccal ganglia situated in the nerve ring rather than more posteriorly. Most subsequent workers have considered the two genera as distinct with the exception of Thompson (1975:500) who stated that "the distinction is based upon several features of the morphology which appear to me inadequate," but provided no further details. Most recently, Valdés (1996) provided phylogenetic evidence that species of *Doriopsilla* and *Dendrodoris* form monophyletic sister clades. The present species possess the synapomorphic features of an eccentric anus, a flattened prostate, and penial spines with an elongate base, which characterize members of *Doriopsilla* (Valdés & Ortea, 1997).

Systematic confusion has surrounded the systematics of the Dendrodorididae from the Pacific coast of North America. Cooper (1863) described *Doris albopunctata* from Santa Barbara, California. Only the external coloration was described and no type material is extant (MacFarland, 1905). MacFarland (1905) later described *Doriopsis fulva* from Monterey Bay, California. Similarly, he described only the external anatomy and coloration of the living animal. In his original description, MacFarland noted that *D. fulva* was possibly identical with Cooper's species, but stated it was difficult to be certain, based on the superficial description and the absence of Cooper's type material. Subsequently (1906), he described and illustrated aspects of the reproductive system of *D. fulva*. Cockerell & Eliot (1905) described *Doridopsis reticulata* from San Pedro, California. They described the external morphology and a few aspects of the internal anatomy. They also stated that their species might be identical to *Doris albopunctata* Cooper. Steinberg (1961) considered these three species as synonymous, the differences being based largely on a darker coloration of spec-

imens from southern California. Roller (1970) and McDonald (1983) also considered these three names as synonyms. Behrens (1980, 1991) considered *Dendrodoris fulva* as distinct from *Doriopsilla albopunctata*. Our examination of specimens of *Doriopsilla albopunctata* from Baja California to northern California revealed considerable variation in the body color, similar to that described by Steinberg (1961). Specimens from northern California are light yellow throughout, but may occasionally have a central patch of chestnut brown on the dorsum. Specimens from southern California exhibit much more variation in color than do northern California specimens, but are generally much darker in color. There were no other significant anatomical differences between specimens of different color forms or from different localities. All specimens with white gills produced egg masses with a spiral attached to the substrate by its inner edge. All of these egg masses yielded planktrophic larvae. Analysis of allozyme frequencies yielded no significant differences within or between widely separated populations. Analysis of morphological, developmental and genetic data support the conclusions of Steinberg (1961), Roller (1970), and McDonald (1983), that *Doris albopunctata* Cooper, 1863, *Doriopsis fulva* MacFarland, 1905, and *Doridopsis reticulata* Cockerell & Eliot, 1905, represent a single species with Cooper's name having priority as the senior synonym. There is no doubt that the material described by Cockerell & Eliot (1905) and MacFarland (1906) are conspecific with the present material. Cockerell & Eliot described an elongate receptaculum seminis (as "spermatocyst") as in the present material. MacFarland (1906:fig. 38) illustrated part of the reproductive system of *Doriopsis fulva* with a receptaculum seminis (as "spermatocyst") which exceeds the length of the bursa copulatrix (as "spermatheca") and which enters the vagina proximally, as in the present material.

Material that Behrens (1980, 1991), McDonald & Nybakken (1980), and McDonald (1983) considered as a distinct species is conspecific with *Doriopsilla gemela*.

Doriopsilla gemela is morphologically distinct from *D. albopunctata*. Externally, specimens of *D. gemela* have deep yellow or yellow-orange gills, whereas those of *D. albopunctata* are white or pale yellow. There are fewer rhinophoral lamellae (7–10) in *D. gemela* than in *D. albopunctata* (11–30). The larger tubercles of *D. albopunctata* contain glands, whereas the smaller ones of *D. gemela* do not. The remainder of the external anatomy is extremely similar between the two species.

The internal anatomy of the two species differs consistently in many significant regards. The glandular portion of the esophagus of *D. gemela* is more elongate and convoluted than in *D. albopunctata*. More posteriorly, *D. gemela* has an elongate muscular portion of the esophagus, while that of *D. albopunctata* is short. The digestive gland lobes are well separated and lobed on the outer edges in *D. gemela*, while they are partially fused in *D.*

albopunctata. The intestinal caecum is readily visible in *D. gemela*, but is more ventral and obscured by the glandular portion of the intestinal lobes in *D. albopunctata*.

There are also consistent differences in the reproductive anatomy of the two species. The ejaculatory portion of the vas deferens of *D. gemela* is elongate and consists of many convolutions, whereas in *D. albopunctata* the ejaculatory segment is shorter and thicker and without convolutions. In *D. gemela* there are about six rows of small penial spines that are 15–20 µm in length. In contrast, in *D. albopunctata* there are about 16 rows of spines that are about 50 µm in length. The receptaculum seminis of both species is fairly elongate, but in *D. albopunctata* it is more elongate and extends beyond the proximal extreme of the bursa copulatrix. More significantly, the duct of the receptaculum seminis of *D. gemela* enters the distal portion of the vagina, while in *D. albopunctata* it enters the proximal extreme, near the base of the bursa copulatrix.

The two species differ markedly in their developmental biology. In *D. gemela* the egg ribbon is flat against the substrate, while in *D. albopunctata* it is attached by its narrow edge and well elevated from the substrate. In *D. gemela* the yolky eggs develop into lecithotrophic larvae, while the larvae of *D. albopunctata* are planktotrophic. Genetic distances in allozyme frequencies are also consistent with distinct congeners.

Among described species of *Doriopsilla*, *D. gemela* is unique in having the receptaculum duct enter the vaginal duct basally. The presence of an elongate muscular portion of the esophagus is identical to that described for *D. rowena* Marcus & Marcus, 1967 (Marcus & Marcus, 1967:206, fig. 62b), rather than a short muscular portion described here for *D. albopunctata* and previously for *D. janaina* Marcus & Marcus, 1967 (Gosliner, 1991:292, fig. 8). These differences in digestive anatomy between *D. gemela* and *D. albopunctata* suggest that despite their similarity in external morphology and coloration, they are both anatomically more similar to other species than to each other. Morphological data from other species of *Doriopsilla* is necessary to develop hypotheses of phylogeny and test the suggestion that *D. gemela* is more closely related to *D. rowena* than to *D. albopunctata* and *D. janaina*.

Valdés & Ortea (1997) suggested that *Doriopsilla rowena* and *D. janaina* might be possible synonyms of *D. areolata* Bergh, 1880. However, *D. janaina* differs from *D. areolata* in having a short rather than elongate muscular portion of the esophagus (Gosliner, 1991). Based on the description of Marcus & Marcus (1967:fig. 62c), *D. rowana* differs from *D. areolata* in that the duct of the receptaculum seminis is separated from the bursa copulatrix, whereas in *D. areolata* it enters directly at the base of the bursa (Valdés & Ortea, 1997:fig. 4b). The color patterns of these species also differ from the variation described for any of the subspecies of *D. areolata*. It

would appear that *D. rowena* and *D. janaina* represent distinct species.

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Observations on the Embryonic Development of *Octopus mimus* (Mollusca: Cephalopoda) from Northern Chile

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Abstract. The embryonic development of *Octopus mimus* Gould, 1852, was studied under normal upwelling temperature conditions (16°C) and under conditions of medium and strong El Niño Southern Oscillation (ENSO) events (20°C and 24°C, respectively). The embryonic development under high temperature conditions is faster than at lower temperature. Embryonic development of *Octopus mimus* under normal upwelling temperature conditions (represented by a constant temperature of 16°C) takes about 35% more time than under conditions of medium ENSO events (at a constant temperature of 20°C), and 62% more on average than under conditions of strong ENSO events (at a constant temperature of 24°C). There were no abnormalities visible on the embryos developed at 24°C. The hatching rate was high (estimated at about 95%). The higher temperature had no adverse effect on the viability of the hatchlings. This suggests genetic fixation of a wide temperature tolerance.

The embryonic development of *Octopus mimus* is very similar to that of *O. vulgaris* Cuvier, 1797. However, egg and hatchling size, number of gill lamellae per demibranch, and heartbeat frequencies differ between the two species.

INTRODUCTION

Octopus mimus Gould, 1852, is common along the Chilean coast from 18°S to 37°S (Osorio et al., 1979). This octopus is an important resource for artisanal fisheries in the northern part of Chile. From 1978 to 1994 the total catch increased from 4 tons to 3732 tons (Servicio Nacional de Pesca, 1994).

During El Niño Southern Oscillation (ENSO) conditions in 1982/1983, the population size of *Octopus mimus* increased significantly, in contrast to most other invertebrates of this region which died out or were significantly reduced (Arntz & Fahrbach, 1991). Near Antofagasta (northern Chile) the population of *O. mimus* increased by a factor of 100 (Tomicic, 1985).

Little is known about the life cycle of *Octopus mimus*. Size at maturity and the reproductive cycle were studied by Arancibia (1984) and Cortez et al. (1995b). Wolff & Perez (1992) investigated aspects of population dynamics, food consumption, and conversion efficiency, and Cortez et al. (1995a) observed feeding dynamics. *Octopus mimus* was long synonymized with *O. vulgaris* Cuvier, 1797, and has only recently been recognized again as a separate species (Guerra et al., personal communication). Apart from a few pictures of an egg mass given by Cortez (1995), nothing has been published on the embryonic development of *O. mimus*. The present study provides details of the embryonic development, under normal upwelling conditions (16°C) and under conditions of medium and strong ENSO influence (temperature 20°C and 24°C, respectively). The aims of this study are (1) the assessment of the influence of ENSO type temperature

changes on embryonic development, and (2) to define the differences in embryonic development between *O. mimus* and *O. vulgaris*.

METHODS

Adult *Octopus mimus* were collected off the coast of northern Chile in the region of Iquique, by SCUBA diving at depths of 5–10 m. Dorsal mantle length (measured from the midpoint between the eyes to the apex of the mantle tip), head width, and weight were determined in all adult females. In the field, the main spawning season of *O. mimus* is between November and March, although egg laying is observed throughout the year. Animals were maintained in 500 L tanks at the Departamento Ciencias del Mar (Universidad Arturo Prat). All octopuses were kept in the laboratory under constant temperature conditions of 16°C, 16.5°C, 20°C, and 24°C ($\pm 1^\circ\text{C}$) with a slow continuous flow of clean seawater resulting in a daily renewal of the whole water volume.

The nitrate content of the aquarium water was monitored following the recommendation of Boletzky & Hanlon (1983). When a high nitrate concentration was observed, the aquarium water was partly changed until nitrate could no longer be detected.

Females were kept isolated in covered tanks. Each tank contained a clay flower pot as a hiding place for the female, providing her with a substrate on which she could attach her eggs and brood them as she would do in a den under natural conditions.

Brooding females of *Octopus mimus* were fed daily at least one item from a variety of clams (*Venus antiqua*,

Protothaca thaca, *Gari solida*, and *Tagelus dombii*), and crabs (*Leptograpsus variegatus* and *Cancer setosus*). *Venus antiqua* was the dominant food item.

The females laid their eggs in long strings or festoons. The number of strings was counted and the string length was measured. The number of eggs in 1 cm of string was determined, providing an estimation of total egg number per egg mass. At 3-day intervals, 3–10 eggs were removed from each egg mass and examined under a dissecting microscope. Drawings were made, and photographs of the eggs were taken with a camera (Nikon System of Microflex HFM-35A-35 mm camera box M35FA) connected to the dissecting microscope (Nikon SMZ-10). A video camera (Sony video color 1 CCD model DXC107A) attached to the microscope was used occasionally to monitor embryos.

Eggs were fixed in Bouin's fixative (15 vols. picric acid, 5 vols. formalin, 1 vol. acetic acid) and preserved in 70% ethanol for later examination. Developmental stages of the embryos were identified according to Naef (1928). The rate of embryonic growth was determined by regular control measurements of egg size, yolk volume, and size of the embryo body. The standard deviation (SD) of size was calculated for each sample size (n). The time required for embryonic development was determined for the different temperatures, along with the frequency of heartbeat at advanced stages. Embryonic mortality within an egg mass was estimated based on the daily observation records. In addition, embryonic development was described and compared to the observations reported for other species of *Octopus* (Boletzky, 1967, 1969, 1971a, b, 1987, 1989; Fioroni, 1978; Hochberg et al., 1992; Joll, 1978; Mangold-Wirz, 1983).

The size of hatchlings, total length, dorsal mantle length, and head width were measured following Hochberg et al. (1992) and standard deviations were calculated. For close observation of behavior, groups of 100 hatchlings each were maintained in six small glass aquaria equipped with air bubblers surrounded by fine mesh to avoid damage to the hatchlings. Each aquarium contained 55 L of still seawater, which was changed once a day. The hatchlings were fed various planktonic organisms (mainly larvae of *Pagurus* sp. and of *Cancer setosus*). First feeding was observed through the transparent aquarium wall and was subsequently validated by close inspection of the digestive tract of the observed individuals under the dissecting microscope.

RESULTS

The smallest mature female *Octopus mimus* found during this study in the field had a mantle length (ML) of 120 mm and a head width of 45 mm, with a total wet weight of 868 g. The ovary weighed 165 g; the capsule length of the mature ovarian eggs measured 1.95 mm. The larg-

est female *Octopus mimus* observed weighed 2818 g with a mantle length of 230 mm, and a head width of 50 mm.

Brooding females were fed daily. All females survived for at least 2 weeks after hatching of the last young.

Egg and string size. Egg laying was observed nearly throughout the year (see Table 1). From the egg string counts and subsamples of eggs, the average fecundity of a female *Octopus mimus* was estimated at between 60,000 and 200,000 eggs. Indeed each female laid about 200 strings of eggs ranging from 3–10 cm in length and containing an average of 100 eggs in 1 cm.

The eggs of *Octopus mimus* are small in terms of both absolute and relative size. The chorion capsule of freshly laid eggs measured on average 2.03 mm in length (n = 50; SD = 0.25) and 0.9 mm in width (n = 30; SD = 0.08); the stalk measured 5.7 mm (mean of five measurements) in length (cf. Mangold-Wirz 1983: fig. 21.2 for *O. vulgaris*). The yolk mass on average was 1.7 mm long (n = 27; SD = 0.17) and 0.8 mm wide (n = 27; SD = 0.09). The increase of chorion length through embryonic development was similar in all egg masses except "C" and "F" (Table 1). The value for egg mass "C" is not significant, however, given the small sample size (see Table 1). In this case, the initial chorion length was relatively small compared to the other egg masses. Thus the average increase of chorion length of all egg masses, excluding egg mass "C", was about 11%. There was no correlation between magnitude of size increase and temperature. The hatchlings measured on average 2.34 mm (n = 60 individuals; SD = 0.19) in total length. The range of variation in the hatching size was 2.1–2.6 mm total length. Hatchlings had an average mantle length of 1.85 mm (n = 30; SD = 0.08) and a head width of about 0.84 mm (n = 30; SD = 0.09).

Embryonic development. The embryonic development of *Octopus mimus* (Figure 1A–F) turned out to be very similar to that of *O. vulgaris* (Boletzky, 1969, 1971a, 1989). Like other cephalopods, *O. mimus* develops a discoblastula at the animal pole of the ovum on the side of the micropyle. Stage I of Naef is defined as the end of cleavage (Figure 1A). Then the prospective yolk sac envelope grows over the yolk surface toward the vegetal pole. At Stage VII the first relief elevation of the embryo in the mantle region is visible at the animal pole (Figure 1B). By this time, aided by the ciliary beat of the yolk sac envelope, the embryos begin to rotate around their longitudinal axis in a clockwise direction (in apical view). Eventually the direction of the ciliary beat changes and the embryos reverse their position in the chorion, as described for *Octopus vulgaris* (Boletzky, 1971a, b). The yolk envelope is completed at about Stage IX and the resulting outer yolk sac begins to pulsate irregularly (about seven beats per minute). At Stage X to XI the arm buds are conspicuous but the mantle rudiment is still flat (Figure 1C). The inner yolk sac shows two posterior lobes at about Stage XII. In the depression between these lobes

Table 1

Duration of embryonic development to the day of hatching and growth of *Octopus mimus* during embryonic development under the influence of different temperatures (n = sample size; SD = standard deviation).

Temperature (°C)	Egg mass (date)	Time to first regular heartbeat (days)	Duration of embryonic development to the day of hatching (days)	Length of egg at beginning of embryonic development (mm; mean value)	Total length of hatchling (mm; mean value)	Increase in chorion length during embryonic development
24	A 5/8/95-6/2/95 autumn	18	25	2.11 n = 10 SD = 0.11	2.23 n = 30 SD = 0.20	5.7%
20	B 9/18/94-10/26/94 spring	23	38	2.28 n = 7 SD = 0.22	2.37 n = 10 SD = 0.44	4.0%
20	C 12/12/94-1/24/95 summer	28	43	1.69 n = 2 SD = 0.58	1.96 n = 1	15.98%
20	D 3/20/95-4/26/95 autumn	22	37	2.27 n = 10 SD = 0.05	2.42 n = 9 SD = 0.09	6.6%
16.5	E 4/28/95-6/30/95 autumn	46	63	2.06 n = 10 SD = 0.10	2.15 n = 10 SD = 0.04	4.3%
16	F 2/2/95-4/10/95 summer/autumn	44	67	1.78 n = 10 SD = 0.16	2.0 n = 10 SD = 0.15	12.3%

the stomach rudiment has been closed (Figure 1D). The coordination and the first regular pulsation of systemic heart and branchial heart occurs at about Stage XV; it was observed after 18 days (d) at a temperature of 24°C, after 24 d at 20°C (average of two egg masses), and after 44 d at 16°C (Table 1). By stage XV the inner yolk sac is very reduced (Figure 1E) as in other octopods (Boletzky, 1975; Joll, 1978); it increases again later (Figure 1F). The outer yolk sac is now clearly demarcated from the body of the embryo. Before hatching, i.e., between Stage XIX and Stage XX when the outer yolk sac has been strongly reduced in size, most of the embryos reverse their position a second time as in *O. vulgaris* (Portmann, 1933).

There are only a few notable differences between the embryos and the hatchlings of *Octopus mimus* and *O. vulgaris*. The hatchlings of *O. mimus* have seven (Figure 1G) gill lamellae per demibranch, while those of *O. vulgaris* have only five (Boletzky, 1969). The appearance of pigment in the ink sac is somewhat earlier in *O. mimus* (Stage XVII) than in *O. vulgaris* (Stage XVIII). The chorion stalk length in relation to the chorion capsule length of *O. mimus* ($\times 2.8$) is also slightly higher than in *O. vulgaris* ($\times 2.5$) (Boletzky, personal communication; cf. Mangold-Wirz, 1983: fig. 21.2 for *O. vulgaris*).

Embryonic development in *Octopus mimus* takes about

65 d under normal upwelling temperature conditions (represented by a constant temperature of 16°C), about 39 d under conditions of medium ENSO events (at a constant temperature of 20°C), and 25 d on average under conditions of strong ENSO events (at a constant temperature of 24°C) (Table 1 and Figure 2). Thus development duration at 24°C was about 60% of that observed at 20°C, which was about 65% of the development time at 16°C.

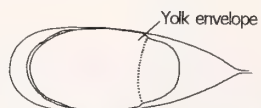
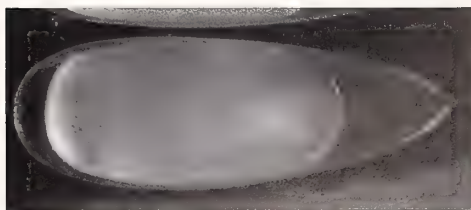
The time lapse between first and last egg laying and between first and last hatching was between 5 and 14 d, respectively, independent of the rearing temperature.

Due to the high room temperature, it was not possible to maintain a constant low water temperature in the Petri dishes used for determination of the heartbeat frequency in embryos when observed under a dissecting microscope. For example, an egg mass kept at an average brooding temperature of 20°C contained embryos showing between 44 and 26 heartbeats/min. Egg mass "E" was kept at a temperature of 16.5°C. At Stage XIX, the heartbeat of an embryo of this egg mass showed a frequency of about 52 pulsations/min. One day later, at a constant temperature of 22°C, the same embryo had a frequency of 94 pulsations/min. This variation is most likely due to the temperature sensitivity of heartbeat rate.

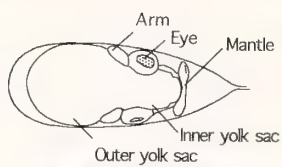
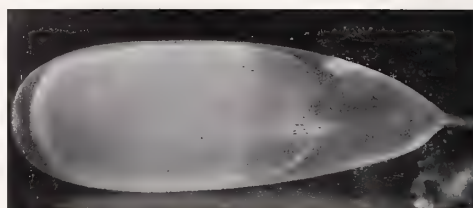
Nevertheless, heartbeat frequency increased with developmental progress in general, until it became relatively



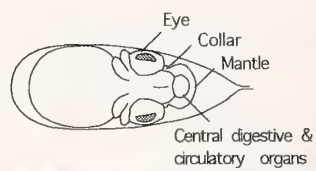
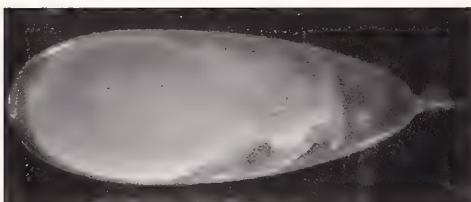
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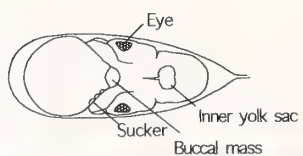
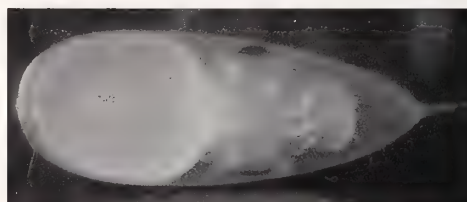
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C



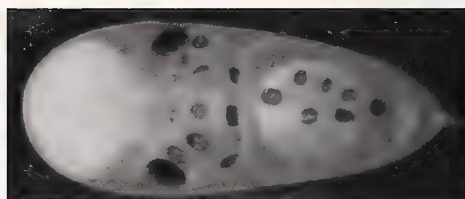
D



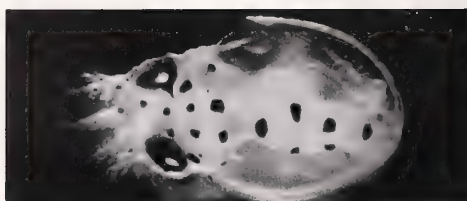
E



F



G



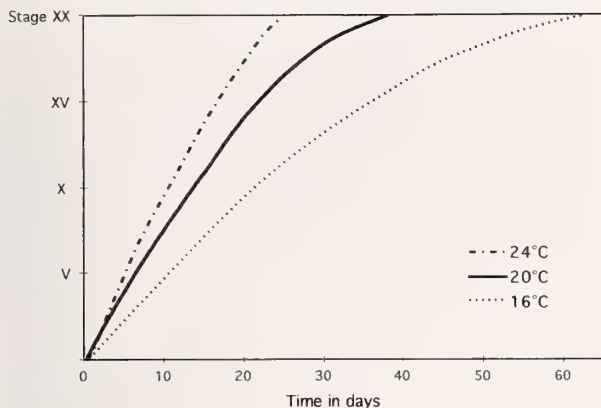


Figure 2

Course of embryonic development in *Octopus mimus* at three different temperatures (stages according to Naef, 1928).

stable from Stage XV onward. In autumn (March until May 1995), the environmental temperature of 20°C corresponded to the brooding temperature of the egg mass "I" during the entire time of embryonic development. At Stage XIII, the average heartbeat was 28 pulsations/min. At Stage XVIII, the heartbeat was about 77 pulsations/min.

The estimated mortality rate of egg masses reported in this paper was low (about 5-20%). The hatching rate of egg masses "B" (20°C) and "A" (24°C) was nearly 100%. Egg mass "E" had fungi on the chorion surfaces, and the mortality rate was more than 50%. After Stage XV, some abnormal stages were visible within this egg mass. The inner yolk sac increased to an abnormally large size. Therefore the data from these embryos are not included in this paper.

Pigmentation. The retina became light orange at Stage X, turned bright red at Stage XIII–XIV (Figure 1E), and finally became dark brown at Stage XVII/XVIII (Figure 1F).

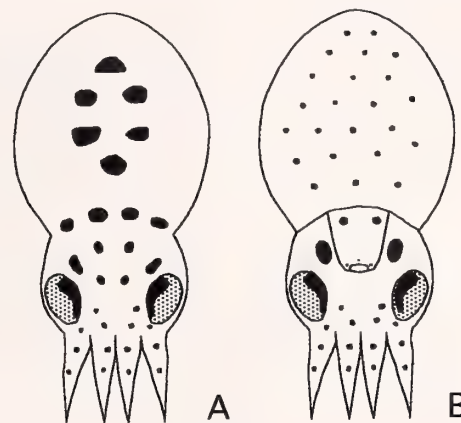


Figure 3

Schematic presentation of chromatophore distribution in *O. mimus* (A = dorsal view, B = ventral view).

Chromatophores appeared at Stage XV on the head, arms, ventral mantle surface, and on the dorsal surface of the visceral mass (bottom of dorsal mantle cavity). The hatchling chromatophore pattern was nearly complete at Stage XIX (Figure 1F). Hatchlings (Figure 3) have a total of 75–89 chromatophores. Every arm has two to four chromatophores on the outside in a simple row. The dorsal surface of the digestive complex has six to eight large visceral chromatophores. The dorsal head surface has 9–10 chromatophores in a 2 + 4 + 4 pattern and one large chromatophore per eye. The ventral head surface has two large chromatophores. The funnel shows five (six) chromatophores in a 3 (4) + 2 pattern. The ventral mantle is evenly covered with 21–24 chromatophores.

Hatchlings. The hatchling size (ML 1.85 mm) is less than 2% (1.15%) of the size of the adult animals (ML 175 mm). Like the hatchlings of other octopodid species producing relatively small eggs (hatchling ML smaller than 8% of adult ML; Boletzky, 1984), the mode of life

Figure 1

Living embryos of *Octopus mimus* (egg size 2 × 1 mm) at different stages of development according to Naef (1928). A. Stage I at the animal pole of the chorion: the end of blastulation is visible (arrow). B. Stage VII: yolk envelope is growing (4/5) over the yolk toward the vegetal pole. At the animal pole the first relief in the mantle region is visible. C. Stage X to XI: dorso-ventral view: after first reversion of the embryo, midgut gland region with huge yolk papilla: clasp of midgut is still open, arm buds conspicuous, mantle rudiment still flat, beginning of retina pigmentation. D. Around Stage XII: arm buds are still rounded, not pointed, inner yolk sac still with two lobes, in the indentation between the lobes the stomach has been closed; the retina is well pigmented, behind the cheek hump the funnel pouches are visible. E. Both animals at Stage XV: lateral view: oval rhomboid retina (red retinal pigment); dorsal view of buccal complex between arms, right dorsal arm with sucker rudiments, inner yolk sac reduced, at this stage regular heartbeats. F. Stage XVIII/XIX: dorsal view: shortly before the second reversion, six to eight chromatophores on dorsal surface located on visceral mass (bottom of dorsal mantle cavity), dorsal head with 10 chromatophores in a 2 + 4 + 4 pattern, each arm with a single row of two to four chromatophores. G. Hatchling of *Octopus mimus* (2.2 × 0.84 mm), note gill with seven lamellae per outer demibranch.

of hatchlings of *O. mimus* is initially planktonic. They have relatively short arms. The longest arms (about 0.9–1.0 mm, $n = 3$) measure about one half the mantle length of the hatchling. The arms of the hatchlings are subequal in length and every arm has three suckers of similar size.

After 4 d of hatching, the inner yolk sac was almost totally absorbed. In the surviving paralarvae, feeding began 5 d after hatching. Larvae of *Pagurus* sp. and of *Cancer setosus* were successfully captured by the hatchlings. *Cancer setosus* clearly acted as a stimulus for feeding as indicated by Villanueva (1994). *Pagurus* sp. and *C. setosus* are very abundant littoral species in the northern part of Chile and thus appear as an appropriate food source. However, survival of young *Octopus mimus* was very limited under aquarium conditions. The last paralarva died 12 d after hatching.

DISCUSSION

Recent morphological investigations (Guerra et al., personal communication; Hochberg & Mangold, personal communication) and DNA-sequencing results (Söller et al., work in progress.) indicate that *Octopus mimus* and *O. vulgaris* are closely related, but distinct species. It appears that their embryonic development is rather similar. Therefore the staging system of Naef (1928) for embryonic development of *O. vulgaris* can be applied to all stages of *O. mimus*. The first and second reversion, the earliest pulsation of the outer yolk sac, and the beginning of the heartbeats occur at the same development stages. Also the stage when pigmentation begins to be visible in *O. mimus* and *O. vulgaris* is the same. In contrast to the chromatophore pattern of *O. mimus* as described by Cortez (1995), I found no clear difference between the chromatophore patterns observed in *O. mimus* and those described by Fioroni (1965) for *O. vulgaris*, since there is always a relatively high natural variability in the respective patterns.

A clear difference was observed in the number of gill lamellae per demibranch at the time of hatching: five for *Octopus vulgaris* (adult: eight to ten [Boletzky, 1969]) and seven for *O. mimus* (adult: seven to eight [Cortez, 1995]). The hatchlings of *Scaevargus unicolor* delle Chiaje, 1830, also have seven lamellae per demibranch of the gill; they are in the same size range, but have four instead of three suckers and more numerous chromatophores than *O. mimus* (Boletzky, 1984). Another distinction between *O. mimus* and *O. vulgaris* is the earlier appearance of the ink in the sac in *O. mimus*. The arm length of *O. mimus* was found to range from 0.9–1.0 mm (measurements from fresh animals), which is somewhat longer than that reported for *O. vulgaris* (0.7 mm; see Hochberg et al., 1992). This slight difference in the arm length is probably insignificant due to the small number of individuals measured ($n = 3$). The chorion stalk length in relation of chorion capsule length of *O. mimus* ($\times 2.8$)

is also slightly larger than that of *O. vulgaris* ($\times 2.5$) (Boletzky, personal communication; cf. Mangold-Wirz, 1983, fig. 21.2 for *O. vulgaris*).

At Stage XVIII, the heartbeat of *Octopus mimus* was about 77 pulsations/min at a temperature of 20°C. This is comparable to *O. tetricus* Gould, 1852, with 65–75 beats/min at a temperature of 19.5°C at Stage XVIII–XIX (Joll, 1978). The stages of the embryonic development of *O. tetricus* are also similar to *O. vulgaris*.

The embryonic development of *Octopus mimus* under high temperature conditions is faster than at lower temperature. Higher temperatures appeared to be of no disadvantage to the hatchlings. Indeed there was no visible difference in hatching success between 20°C and 24°C, the hatching rate in egg masses “B” (20°C) and “A” (24°C) being nearly 100%.

The low survival rate of the hatchlings could be related to failures in the system used for preparing the seawater for the small culture aquaria, and/or to the limited variety of natural food items available. Whether the rather small average increase of egg size in *Octopus mimus* (chorion capsule length 11% for *O. mimus* in these experiments in contrast to 25% for *O. vulgaris*; Boletzky, 1969) is a normal feature or reflects a less than optimal water quality remains to be seen. In any event, embryonic development appeared perfectly normal (except in egg mass “E”; these abnormal embryos are not considered in the results of this paper).

Compared to the developmental rates in *Octopus vulgaris* at a variety of temperatures (Boletzky, 1987), the speed of embryonic development of *O. mimus* is not significantly different. It is within the normal range determined for other warm water octopods with planktonic young, such as *O. cyanea* Gray, 1849, *O. tetricus* and *O. bimaculatus* Verrill, 1883, (see Boletzky, 1969).

Tomicic (1985) described an increase of the population of *Octopus mimus* by a factor of 100 in northern Chile during the last major ENSO event 1982–1983. Thus, *O. mimus*, which is clearly adapted to life in the cold upwelling waters off Chile, can also live under warm water conditions. This population increase may be due to several factors—environmental ones such as decrease in numbers of predators or increase of food supply—or to intrinsic ones, i.e., genetic factors making the animals more competitive, perhaps through physiological improvement of food conversion at higher temperatures.

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Bathymodiolus (Bivalvia: Mytilidae) from Hydrothermal Vents on the Azores Triple Junction and the Logatchev Hydrothermal Field, Mid-Atlantic Ridge

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Abstract. *Bathymodiolus azoricus* n. sp. is described from the Lucky Strike (31°17'N) and the Menez Gwen (37°50'N) hydrothermal fields on the Azores Triple Junction, Mid-Atlantic Ridge, and another species, *Bathymodiolus* sp. aff. *B. puteoserpentis* from Logatchev (14°45'N) hydrothermal field is treated but not named. Both species are compared with *B. puteoserpentis* Cosel, Métivier & Hashimoto, 1994, from the Snake Pit area (23°22'N), also on the Mid Atlantic Ridge. *B. azoricus* is very variable but well distinguished from *Bathymodiolus* sp. and *B. puteoserpentis* by its almost terminal umbo. The three species differ from the type species *B. thermophilus* principally by the absence of an inner mantle fusion and a very short valvular siphonal membrane. The slight differences between *B. puteoserpentis* and *Bathymodiolus* sp. from the Logatchev field do not warrant separation of the latter on species level. The specific endemism of Mytilidae along the Mid-Atlantic Ridge is discussed.

INTRODUCTION

Bathymodiolus species are mytilid bivalves which live in both hydrothermal vent and cold-seep environments using chemoautotrophic processes for their metabolism (Childress & Fisher, 1992). Since the discovery of *Bathymodiolus thermophilus* Kenk & Wilson, 1985, on the Galapagos Rift in 1977, 11 other species of the genus *Bathymodiolus* have been described from a variety of hydrothermal vent and cold-seep environments of both the Pacific and Atlantic oceans (Cosel et al., 1994; Hashimoto & Okutani, 1994; Cosel & Olu, 1998; Gustafson et al., 1998).

On the Mid-Atlantic Ridge, the vent mytilid *Bathy-*

modiolus puteoserpentis Cosel, Métivier & Hashimoto, 1994, was first collected on the Snake Pit hydrothermal field (23°22'N), in June 1988, during the French HYDROSLAKE expedition (Cosel et al., 1994). Subsequently, *Bathymodiolus*-like mussels were found also on other localities of this ridge.

The next site on the Mid-Atlantic Ridge (further abbreviated as MAR) with a mussel population was discovered in September 1992 at 37°17.6'N by an American expedition, and samples were taken by dredge (Van Dover, 1995). In 1993, more mytilids were collected at the same locality, then called Lucky Strike hydrothermal field (37°17'N, 1640–1700 m) by the submersible Alvin during

Explanation of Figures 1–5

Figures 1–5. *Bathymodiolus azoricus* Cosel & Comtet, sp. nov. Figure 1. Holotype, MNHN, 111.9 mm. PP11 site, Menez Gwen hydrothermal field Mid-Atlantic Ridge, 37°50.5'N, 31°31.3'W, 866 m, DIVA 2, dive 13. Exterior and interior of both valves, dorsal view of specimen and ventral view of right valve to show the position of foot/byssus retractor scars. Figure 2. Paratype, ZMM, 94.3 mm. Same locality. Exterior of left valve. Figure 3. Paratype, MNHN, 109.7 mm. Same locality. Exterior and interior of left valve. Figure 4. Paratype, MNHN, 103.0 mm. Same locality. Exterior and interior of right valve. Figure 5. Specimen from Menez Gwen, same locality, DIVA 2, dive 11, MNHN, 70.4 mm. Exterior and interior of left valve.



the American expedition LUCKY STRIKE 1993 (Van Dover et al., 1996). Additional populations of this mussel were found and specimens collected on a larger scale by the French submersible Nautile during the expeditions DIVA 1 (May 1994) and DIVA 2 (June 1994) of the R/V *Nadir*. During these cruises, also the newly discovered Menez Gwen hydrothermal field (37°50'N, 844–850 m) was studied and mussels were collected (Desbruyères et al., 1994; Fouquet et al., 1995).

Another mussel population was discovered in June 1993 at 29°10'N (3080 m) on the Broken Spur vent field during the ATLANTIS II cruise (Murton et al., 1995). The two examined shells, brought to our attention by Eve Southward, were provisionally identified as *Bathymodiolus puteoserpentis* by the first author.

Vent mussels were also found in July 1994 at 14°45'N by the Russian LOGATCHEV-7 expedition on board the R/V *Professor Logatchev* (Batuyev et al., 1994). A few mussels were sampled by TV-guided bottom grab. More material, in total 15 specimens, was taken in February 1995 by the Russian submersible Mir-2 during the cruise 35 of the R/V *Akademik Mstislav Keldysh* at 14°50'N. In December 1995, specimens of the same mussel were taken by the French submersible Nautile during the cruise MICROSMOKE at 14°45'N, now called the Logatchev hydrothermal vent field.

The two *Bathymodiolus* species from 37°N (Lucky Strike and Menez Gwen hydrothermal field, Azores Triple Junction) and from the Logatchev hydrothermal field were found to be different from *Bathymodiolus puteoserpentis* and are described in this paper, but only one of them is introduced as a new species. Some ecological and biogeographical remarks on mytilids of the MAR are also given.

MATERIALS AND METHODS

Most of the studied material was collected during the already mentioned French expeditions DIVA 1 and DIVA 2, organized by IFREMER (Institut français de Recherche pour l'Exploitation de la Mer) and MICROSMOKE, organized by the CNRS (Centre National de Recherches Scientifiques). The material was sorted by the Centre Na-

tional de Tri d'Océanographie Biologique (CENTOB), Brest.

Shell lengths and heights were measured using the standards of Kenk & Wilson (1985:fig. 1) in a total of 7832 individuals from both Azores Triple Junction and Logatchev. Anterior part length (i.e., length from the anterior margin to the umbo) was additionally measured on 159 individuals. Data for *Bathymodiolus puteoserpentis* were taken from Cosel et al. (1994) and from measurements of a few additional specimens. All statistical analyses were carried out using StatView II® or Microsoft Excel 5.0.

Abbreviations used in the text: LACM—Los Angeles County Museum of Natural History, Los Angeles; MCZ—Museum of Comparative Zoology at Harvard University, Cambridge, Massachusetts; MNHN—Muséum National d'Histoire Naturelle, Paris, France; NMNZ—National Museum of New Zealand, Wellington, New Zealand; NSMT—Natural Science Museum, Tokyo, Japan; SMF—Natur-Museum und Forschungsinstitut Senckenberg, Frankfurt/M, Germany; USNM—National Museum of Natural History, Smithsonian Institution, Washington, D.C.; ZMM—Zoological Museum of Moscow University. sh.—empty shell; spm.—wet preserved specimen(s); R/V—research vessel; MAR—Mid-Atlantic Ridge.

SYSTEMATICS

Family MYTILIDAE

Genus *Bathymodiolus* Kenk & Wilson, 1985

Bathymodiolus azoricus Cosel & Comtet, sp. nov.
(Figures 1–15, 25–33, 36, 37, 39–52, 59, 60, 62)

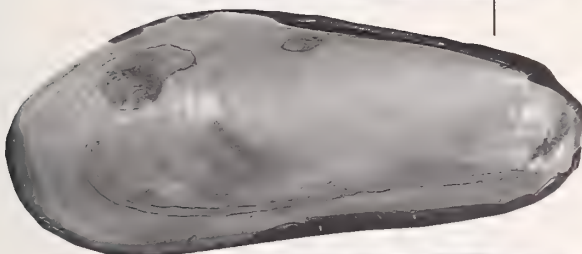
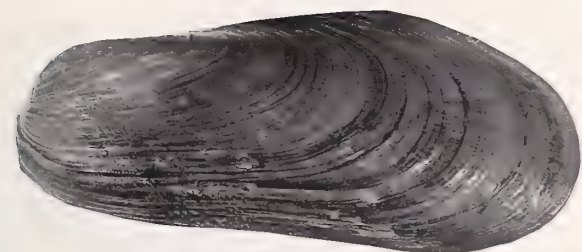
Type material: Holotype, MNHN, Menez Gwen hydrothermal field, Mid-Atlantic Ridge, DIVA 2 expedition, dive 13, A.-M. Alayse, observer, 15 June 1995. 22 paratypes with preserved animal, same locality, 14 in MNHN; 1 in MCZ; 1 in NSMT; 1 in USNM; 1 in LACM; 1 in SMF; 1 in ZMM; 1 in Museum Funchal; 1 in NMNZ.

Type locality: PP11 site, 37°50.5'N, 31°31.3'W, 866 m,

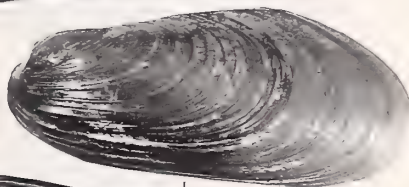
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Explanation of Figures 6–11

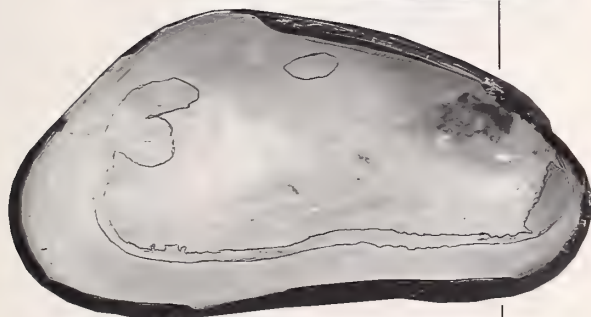
Figures 6–11. *Bathymodiolus azoricus* Cosel & Comtet, sp. nov. Figure 6. Specimen from Lucky Strike hydrothermal field, 64.0 mm, site Statue of Liberty, 37°17.59'N, 32°16.50'W, 1635 m, "LUCKY STRIKE 1993" expedition, dive 2605. Exterior and interior of left valve. Figure 7. Specimen from Lucky Strike hydrothermal field, 44.8 mm. Same locality. Exterior and interior of left valve. Figure 8. Specimen from Lucky Strike hydrothermal field, site Pagoda (PP7), 37°17.63'N, 32°16.96'W, 1629 m, DIVA 2, dive 07, 91.1 mm. Exterior, interior, and ventral inner view of left valve. Figure 9. Specimen from Lucky Strike hydrothermal field. Same locality, 59.3 mm. Exterior of right valve. Figure 10. Specimen from Lucky Strike hydrothermal field, site Eiffel Tower, 37°17.32'N, 32°16.52'W, 1685 m, DIVA 2, dive 08, 84.7 mm. Exterior, interior, and ventral inner view of left valve. Figure 11. Specimen from Lucky Strike hydrothermal field, site Elisabeth, 37°17.63'N, 32°16.87'W, 1640 m, DIVA 2, dive 24, 114.1 mm. Exterior and interior of left valve. All specimens MNHN.



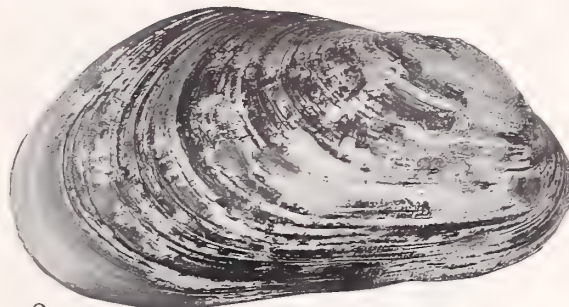
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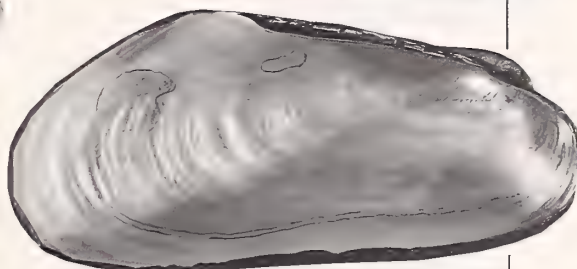
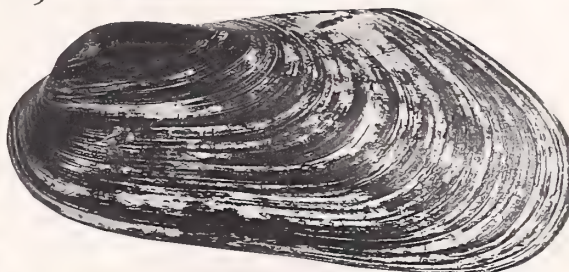
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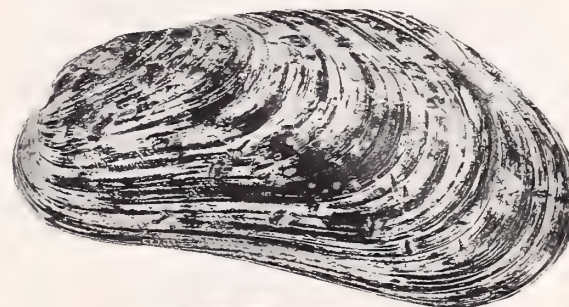
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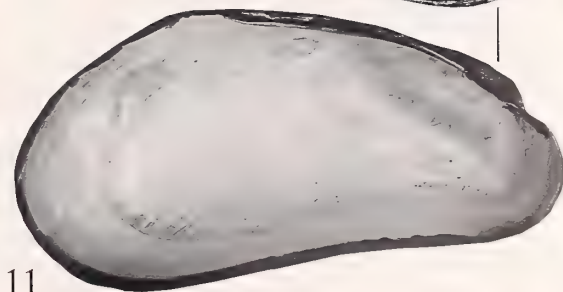
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11



Menez Gwen hydrothermal field, Azores Triple Junction, Mid-Atlantic Ridge.

Description: Shell up to 119 mm long, more or less elongate-modioliform, from thin but solid to rather thick, extremely variable in outline and length/height ratio, but also in tumidity and shell thickness, equivalve, smaller specimens often shorter. Beaks subterminal to almost terminal. Anterior margin more or less broadly rounded; ventral margin in juvenile, half-grown, and subadult specimens mostly more or less convex or straight, in fully grown specimens straight or more or less concave. Postero-ventral margin evenly rounded, postero-dorsal margin slightly to markedly convex, occasionally straight; postero-dorsal corner rounded; ligament plate usually slightly arched but occasionally almost straight. Exterior with more or less dense, irregular growth lines and growth waves, more or less reflected on interior (see Figures 1 and 10). Some specimens have about five to six broad and very obscure transverse waves in middle of shell which cause occasionally undulation of concentric striae and may be marked by darker color of periostracum; they are reflected as very flat and indistinct waves on interior (see Figure 4). In very few specimens, sculpture of faint, broad, radial and sometimes bifurcating undulations visible on postero-dorsal slope slightly visible on Figure 6; it may be very slightly reflected on inside. Umbo broad, somewhat flattened.

Shell without periostracum dull whitish; interior nacreous white.

Periostracum strong, warm chestnut brown, in umbonal region and often also lighter brown postero-dorsally; smaller specimens especially often appear more or less two-colored with antero-ventral part dark chestnut brown and postero-dorsal part lighter olive brown with relative sharp limit reaching from umbonal region to postero-ventral corner or just in front of it. Surface somewhat dull, with no periostracal hairs; however, byssal endplates of other specimens scattered over whole valve.

Hinge edentulous, anterior hinge margin, however, slightly protruding toward ventral. Ligament opisthodontic, strong, extending over whole postero-dorsal margin nearly to postero-dorsal corner and ending abruptly or in a taper. Subligamental shell ridge hardly marked to obsolete from under umbos to middle of ligament, then missing.

Anterior adductor scar long-oval, arched, situated just in front of umbo. Posterior adductor scar united with posterior scar of posterior pedal and byssus retractor muscle. Anterior scar of same muscle separated and situated under ligament's end or slightly more forward. Anterior byssus retractor muscle scar situated in umbonal cavity, reaching from umbo toward posterior, visible only in posterior and ventral view but not in lateral view of interior. Pallial line ventrally slightly concave or straight.

Examined larval shells (Figures 45–52) measured between 522 and 527 μm long and were nearly 500 μm high. There is a separation between a very small protoconch I (about 110 μm long) and the large protoconch II, which indicates a long planktonic larval phase. Protoconch II pale beige-salmon and well separated from teleoconch which in ultra-juvenile specimens is nearly transparent. Surface of protoconch II with fine regular concentric grooves which are more or less densely spaced, protoconch I with irregular sculpture.

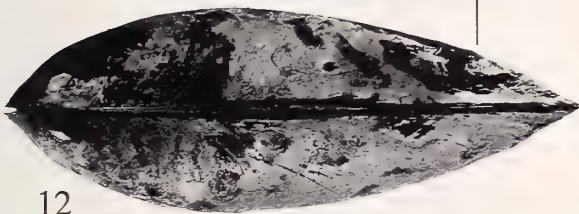
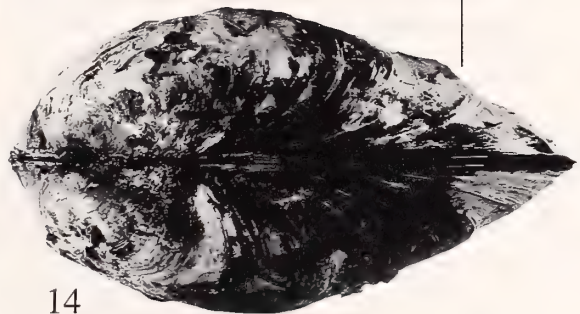
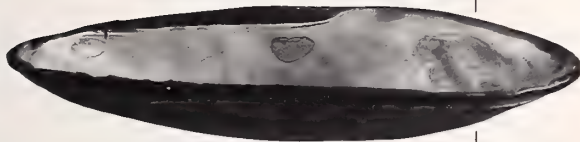
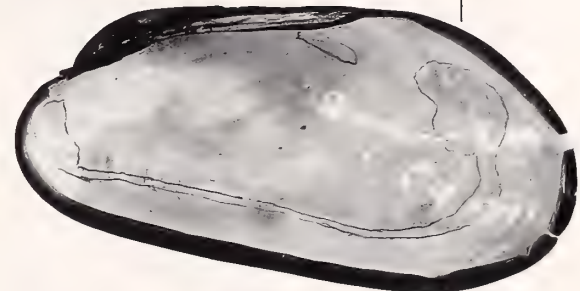
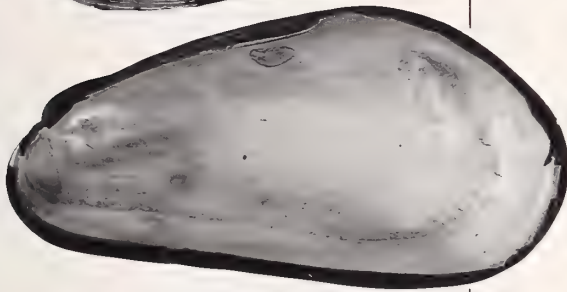
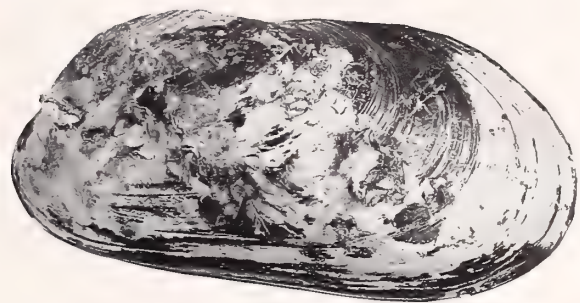
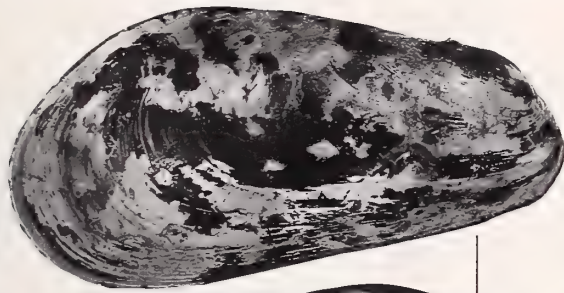
Animal with very large ctenidia which are nearly four-fifths of shell length; outer and inner demibranch almost of equal size, outer demibranch only slightly shorter anteriorly. Ascending lamellae of both demibranchs anteriorly fused to the mantle visceral mass for a very short distance, then becoming free toward posterior. Narrow and well-visible food groove on ventral edge of each demibranch; outer surface of ascending lamellae of inner and outer demibranch with grooves just below free edges and parallel to them. No muscular longitudinal ridge on mantle and visceral mass where dorsal edges of ascending lamellae touch mantle lobes. Connection bars between free edges and gill axes absent. Inner mantle folds separate along whole ventral margin length from anterior adductor to posterior margin. Filaments moderately broad; each fifth to seventh filament with a connecting septum of about half the height of demibranchs.

Mantle lobes thin but with strongly muscular mantle margins. Mantle edges with three folds, inner mantle fold frilled but degree of frilling variable. On anterior end, inner mantle folds pass from ventrally over anterior adductor muscle up- and forward along anterior margin, then fold down- and backward to pass again lower end of anterior adductor muscle or slightly posterior to it toward ventral margin. On this "folding part" mantle edge

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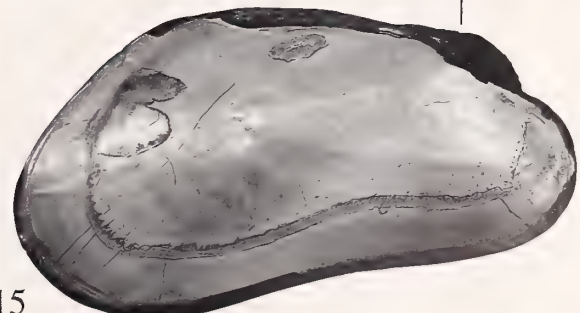
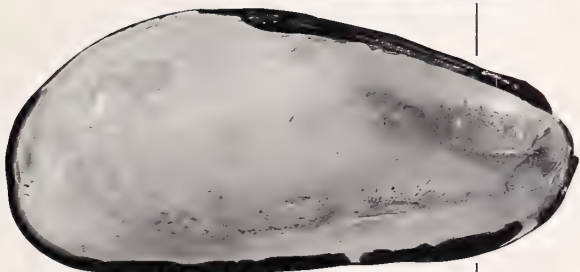
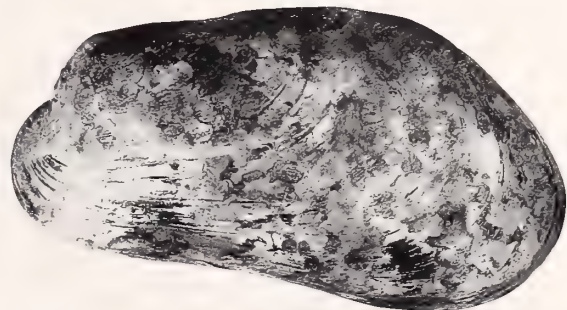
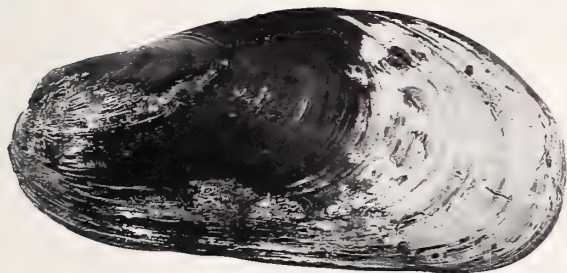
Explanation of Figures 12–15

Figures 12–15 *Bathymodiolus azoricus* Cosel & Comtet, sp. nov. Figure 12. Specimen from Lucky Strike hydrothermal field, site PP5, 37°17.49'N, 32°16.88'W, 1725 m, DIVA 2, dive 05, 83.0 mm. Exterior, interior, and ventral inner view of right valve and dorsal view of specimen. Figure 13. Specimen from Lucky Strike hydrothermal field. Same locality, 63.1 mm. Exterior, interior, and inner ventral view of left valve. Figure 14. Specimen from Lucky Strike hydrothermal field. Same locality, 61.6 mm. Exterior and interior of left valve, dorsal view of specimen. Note the different tumidity of the specimens on Figures 13 and 14 from the same locality. Figure 15. Specimen from Lucky Strike hydrothermal field. Same locality, 90.3 mm. Exterior and interior of left valve. All specimens MNHN.



12

14



13

15

remains frilled (Figure 33), but occasionally is less or not frilled on passage over anterior adductor from one valve to the other (Figures 31, 32). Valvular siphonal membrane short and rather strong, reaching from postero-ventral corner to exhalent siphonal opening, with more or less developed papilla in middle on anterior edge (see Figures 31–33). Inner siphonal aperture with internal diaphragm with horizontal slit and muscular fold around it. Two very broad and short flattened tentacles ventrally under slit, directed toward anus (see Figures 43, 44).

Foot somewhat variable but generally rather small and quite slender, with ventral byssal groove two-thirds to three-fourths length of foot. Foot-byssus retractor muscle complex with rather long anterior retractor; posterior byssus retractors consisting of two quite strong, diverging muscle bundles with common base at base of byssus. Anterior bundle very short and broad and arising rather steeply toward attachment point on shell inside, posterior bundle very long and thin, passing almost parallel to longitudinal shell axis toward attachment point directly in front of posterior adductor. Posterior foot retractor rather thin, arising from base of foot, well in front of base of byssus retractor muscles, passing outer side of anterior retractor toward anterior bundle of posterior byssus retractor; it reaches inner shell surface closely appressed to anterior bundle over half to two-thirds its length. Labial palps variable in size, generally rather large (Figure 42) but in juveniles more or less small, occasionally also in larger specimens (Figure 41). Posterior labial palps narrow-triangular, anterior two slightly smaller than posterior pair and still narrower. Labial palp suspensor muscles present.

Mouth transverse, slit-shaped; esophagus a narrow tube with irregular, close-set longitudinal ridges on its inner surface just in front of entrance to stomach. Stomach (Figure 62) small and very elongate for a mytilid, with thin walls, anterior chamber slightly shorter than posterior chamber but both with about equal width. Digestive diverticula around whole stomach. Style sac and midgut conjoined. Major typhlosole passing from there toward anterior along floor of posterior stomach chamber, and ending in anterior chamber. On left side of posterior chamber, three diverticle ducts open into shallow depression corresponding to left pouch and situated below gastric shield. Small grooves leading from every digestive duct opening and joining to form beginning of intestinal groove. This latter following major typhlosole, turning right and running along right side of it toward and into midgut. Minor typhlosole on right side of midgut and ending just after entering posterior chamber. In this chamber six openings of digestive diverticula ducts. Stomach of examined specimen contained only some mucus. No crystal style found.

Midgut running straight backward to under ventricle, there making very small to moderately large counter-clockwise recurrent loop before entering it just in front of auricular ostiae. Heart with muscular ventricle and

very large auricles which are fused posteriorly under intestine.

Selected measurements (length, height, tumidity) in mm with length-height ratios:

a) Menez Gwen

111.9 × 47.4 × 36.0	Menez Gwen Pl 13	2.4	holotype MNHN
109.7 × 45.8 × 34.7	Menez Gwen Pl 13	2.4	paratype MNHN
109.0 × 49.4 × 41.3	Menez Gwen Pl 13	2.2	paratype USNM
108.7 × 49.6 × 38.2	Menez Gwen Pl 13	2.2	paratype MNHN
108.0 × 45.8 × 39.1	Menez Gwen Pl 13	2.4	paratype MNHN
107.5 × 49.5 × 39.6	Menez Gwen Pl 13	2.2	paratype MNHN
103.0 × 44.1 × 35.7	Menez Gwen Pl 13	2.3	paratype MNHN
100.3 × 42.3 × 37.8	Menez Gwen Pl 13	2.4	paratype MNHN
98.5 × 44.2 × 33.2	Menez Gwen Pl 13	2.2	paratype MNHN
95.8 × 38.0 × 29.4	Menez Gwen Pl 13	2.5	paratype SMF
95.2 × 44.7 × 35.1	Menez Gwen Pl 13	2.1	paratype MCZ
95.0 × 40.0 × 34.9	Menez Gwen Pl 13	2.4	paratype MNHN
94.3 × 44.1 × 35.5	Menez Gwen Pl 13	2.1	paratype ZMM
93.4 × 42.6 × 31.7	Menez Gwen Pl 13	2.2	paratype Funchal Mus.
93.0 × 44.1 × 36.9	Menez Gwen Pl 13	2.1	paratype MNHN
92.7 × 40.3 × 33.2	Menez Gwen Pl 13	2.3	paratype LACM
90.9 × 38.7 × 34.5	Menez Gwen Pl 13	2.3	paratype MNHN
87.6 × 40.4 × 30.0	Menez Gwen Pl 13	2.2	paratype MNHN
83.8 × 36.0 × 28.0	Menez Gwen Pl 13	2.3	paratype MNHN
79.6 × 35.0 × 27.8	Menez Gwen Pl 13	2.3	paratype NSMT
77.7 × 32.1 × 27.6	Menez Gwen Pl 13	2.4	paratype MNHN
76.0 × 32.7 × 25.4	Menez Gwen Pl 13	2.3	paratype NMNZ
62.9 × 30.3 × 25.7	Menez Gwen Pl 13	2.1	paratype MNHN

b) Lucky Strike

119.3 × 52.7 × 46.4 mm	Elisabeth Pl. 24	2.3
113.8 × 56.2 × 45.1 mm	Elisabeth Pl. 24	2.0
101.4 × 45.7 × 38.7 mm	Eiffel Tower Pl 08	2.2
97.0 × 43.5 × 33.4 mm	Eiffel Tower Pl 08	2.2
96.0 × 44.0 × 42.0 mm	pp7 Pagoda	2.2
94.6 × 45.1 × 40.0 mm	Eiffel Tower Pl 08	2.1
94.5 × 42.6 × 37.4 mm	pp7 Pagoda	2.2
91.1 × 47.4 × 37.0 mm	pp7 Pagoda	1.9
90.7 × 40.0 × 34.7 mm	Eiffel Tower Pl 08	2.3
89.4 × 43.3 × 32.0 mm	Eiffel Tower Pl 08	2.1
88.4 × 40.4 × 33.3 mm	pp7 Pagoda	2.2
85.4 × 37.0 × 37.0 mm	pp7 Pagoda	2.3
84.1 × 42.7 × 33.6 mm	Eiffel Tower Pl 08	2.0
82.0 × 38.6 × 32.9 mm	pp7 Pagoda	2.1

81.1 × 37.5 × 31.1 mm	pp7 Pagoda	2.2
76.0 × 37.2 × 31.3 mm	pp7 Pagoda	2.0
71.7 × 40.6 × 31.0 mm	pp7 Pagoda	1.8
67.3 × 29.8 × 28.6 mm	pp7 Pagoda	2.3
61.1 × 28.4 × 24.7 mm	pp7 Pagoda	2.2
52.4 × 28.4 × 25.2 mm	pp7 Pagoda	1.8
57.8 × 30.3 × 27.7 mm	pp7 Pagoda	1.9
47.8 × 25.5 × 24.5 mm	pp7 Pagoda	1.9
44.9 × 23.1 × 17.5 mm	Pl 10 Eiffel Tower	1.9

Material examined: Type material; other material: Mid-Atlantic Ridge, Azores Triple Junction, Menez Gwen hydrothermal field, site PP11, 37°50.5'N, 31°31.3'W, 866 m, DIVA 2, dive 11, M. Biscoito, observer, 14 June 1995, 46 spm.; site Mogued-Gwen (PP10) 37°50.56'N, 31°31.27'W, 877 m, DIVA 1, dive 13, sample 13.6, Y. Fouquet, observer, 21 May 1994, 3 spm.; same locality, DIVA 2 dive 12, D. Desbruyères, observer, 14 June 1995, 15 spm.; Lucky Strike hydrothermal field, site Statue of Liberty, 37°17.59'N, 32°16.50'W, 1635 m, expedition "LUCKY STRIKE 1993," dive 2605, D. Desbruyères and D. Colodner, observers, 31 May 1993, 29 spm.; site Sintra, 37°17.57'N, 32°16.57'W, 1622 m, DIVA 2, dive 02, Ph. Crassous, observer, 4 June 1995, 26 spm., 10 juv. spm.; site Eiffel Tower, 37°17.32'N, 32°16.52'W, 1685 m, DIVA 2, dive 08, Th. Comtet, observer, 10 June 1995,

19 spm.; same locality, dive 10, M.-C. Fabri, observer, 12 June 1995, 25 spm, 10 juv. spm.; site Isabel, 37°17.37'N, 32°16.64'W, 1685 m, DIVA 2, dive 01, A.-M. Alayse, observer, 3 June 1995, 15 spm., 3 juv. spm.; same locality, dive 03, 8 juv. spm.; site Pagoda (PP 7), 37°17.63'N, 32°16.96'W, 1629 m, DIVA 2, dive 06, P. Briand, observer 8 June 1995, 11 spm, 8 juv. spm.; same locality, dive 07, P.-M. Sarradin, observer; 9 June 1995, 37 spm., 2 v. and numerous juveniles; site PP 5, 37°17.49'N, 32°16.88'W, 1725 m, DIVA 2, dive 05, F. Barriga, observer, 7 June 1995, 15 spm, 13 juv. spm.; site Elisabeth 37°17.63'N, 32°16.87'W, 1640 m DIVA 2 dive 24, A.M. Alayse, observer, 30 June 1995, 15 spm., all MNHN.

Biotope: *Bathymodiolus azoricus* dominates the fauna of both the Menez Gwen and Lucky Strike hydrothermal fields. At Lucky Strike, the mussels live byssally attached to hard substrate and cover the walls of active edifices and flanges (on the Pagoda site), where small specimens reach densities up to 10,000 ind/m² (A. Colaço, personal communications). They also colonize cracks in the sea floor. The species lives at temperatures ranging from about 6°C (i.e., the ambient seawater temperature) to about 30°C. The distribution of the mussels along the thermal and chemical gradient seems to be related to their size, the largest individuals living in the warmest areas (Comtet, unpublished data). At Menez Gwen, the colo-

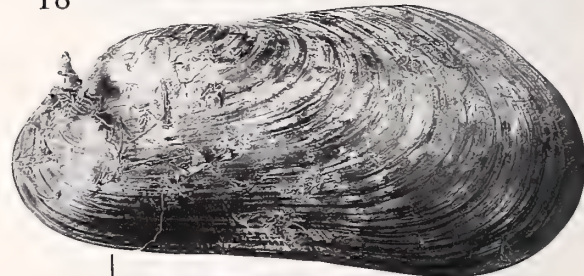
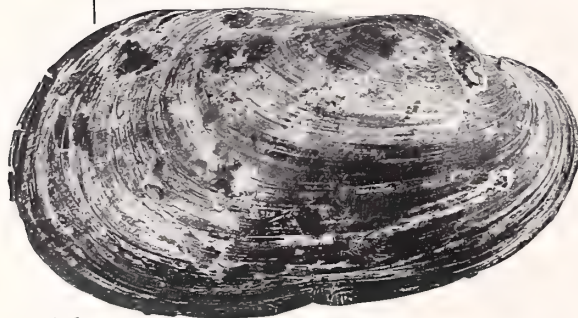
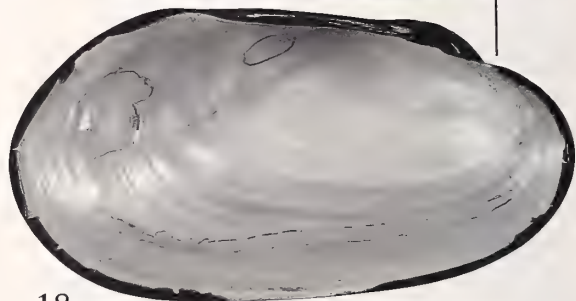
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Explanation of Figures 16–21

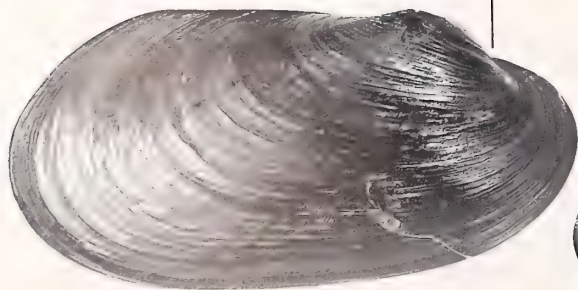
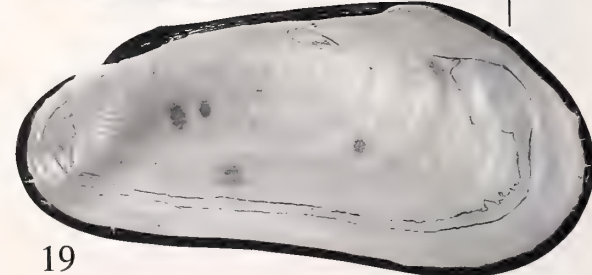
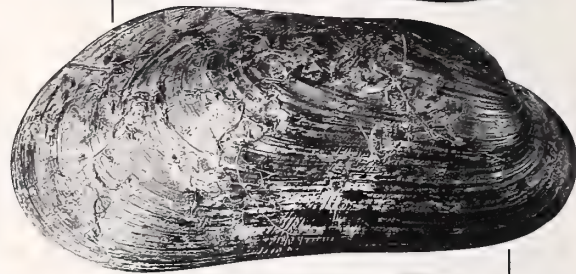
Figures 16–21 *Bathymodiolus* sp. Figure 16. Specimen from Logatchev hydrothermal field, 14°45'N, 44°58'W, 2930–3010 m, cruise 35 R/V *Akademik Mstislav Keldysh*, sta. 3452, ZMM, 61.5 mm, exterior and interior of left valve, exterior of right valve. Figure 17. Specimen from Logatchev hydrothermal field. Same locality, 83.3 mm. Interior and exterior of right valve. MNHN. Figure 18. Specimen from Logatchev hydrothermal field, Irina site 14°45.10'N, 44°48.60'W, 3040 m, MIKROSMOKE, dive 21, 69.1 mm. Exterior and interior of left valve. Figure 19. Specimen from Logatchev hydrothermal field. Same locality, 122.9 mm. Exterior of both valves, interior of right valve. Figure 20. Specimen from Logatchev hydrothermal field. Same locality, 47.5 mm. Exterior of left valve. Figure 21. Specimen from Logatchev hydrothermal field. Same locality, 41.1 mm. Exterior of left valve. All MNHN.

Explanation of Figures 22–30

Figures 22–24 *Bathymodiolus* sp. Figure 22. Specimen from Logatchev hydrothermal field, Irina site, 14°45.10'N, 44°48.60'W, 3063 m, MIKROSMOKE, dive 20, 95.0 mm. Exterior, interior, and inner ventral view of right valve, dorsal view of specimen. Figure 23. Specimen from Logatchev hydrothermal field, Irina site 14°45.10'N, 44°48.60'W, 3040 m, MICROSMOKE, dive 21, 120.3 mm. Exterior and interior of left valve. Figure 24. Specimen from Logatchev hydrothermal field. Irina site, 14°45.10'N, 44°48.60'W, 3063 m, MICROSMOKE, dive 20, 81.7 mm. Exterior of left valve. All MNHN. Figures 25–30. *Bathymodiolus azoricus* Cosel & Comtet, sp. nov. Figure 25. Specimen from Lucky Strike hydrothermal field, site Pagoda (PP7), 37°17.63'N, 32°16.96'W, 1629 m, DIVA 2, dive 07, 44.4 mm. Exterior and interior of left valve. Figure 26. Specimen from Lucky Strike hydrothermal field, same locality, 34.6 mm. Exterior and interior of left valve. Figure 27. Specimen from Lucky Strike hydrothermal field, site PP 5, 37°17.49'N, 32°16.88'W, 1725 m, DIVA 2, dive 05, 47.3 mm. Exterior and interior of left valve. Figure 28. Specimen from Lucky Strike hydrothermal field, site Eiffel Tower, 37°17.32'N, 32°16.52'W, 1685 m, DIVA 2, dive 10, 48.3 mm. Exterior and interior of left valve. Note the highly different height of specimens of the same size. Figure 29. Specimen from Lucky Strike hydrothermal field, site Pagoda (PP7), 37°17.63'N, 32°16.96'W, 1629 m, DIVA 2, dive 07, 16.2 mm. Exterior of left valve. Figure 30. Specimen from Menez Gwen hydrothermal field, site Mogued Gwen (PP10) 37°50.56'N, 31°31.27'W, 877 m, DIVA 2, dive 12, 85.0 mm (details of this specimen shown on Figures 31 and 36). All specimens MNHN.

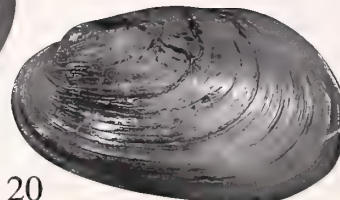


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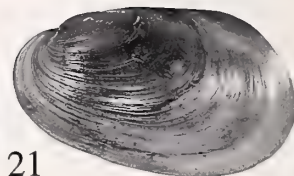


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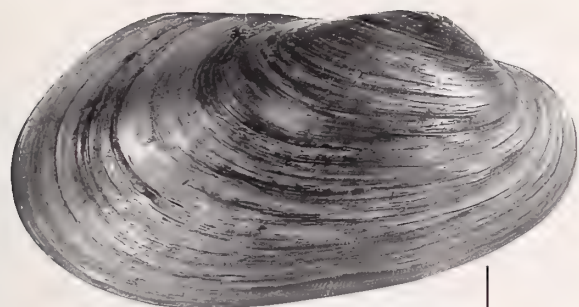
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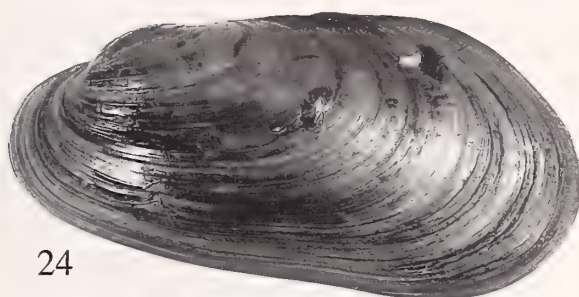
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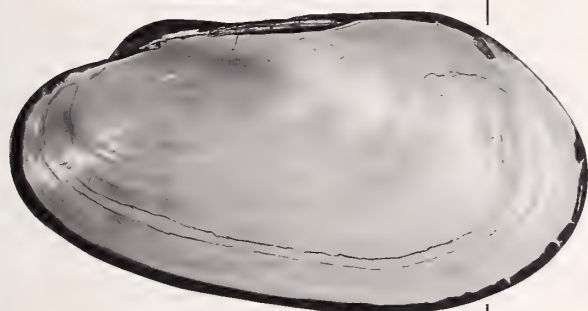
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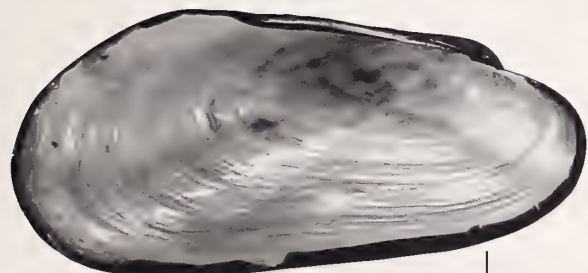
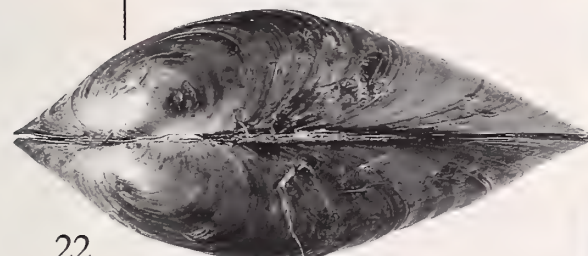
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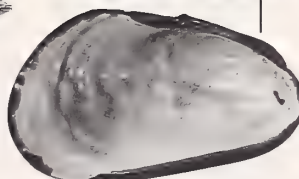
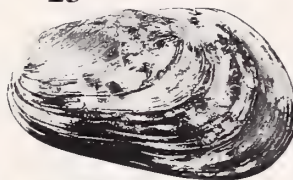
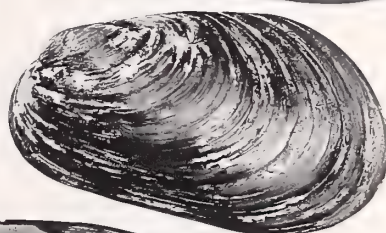
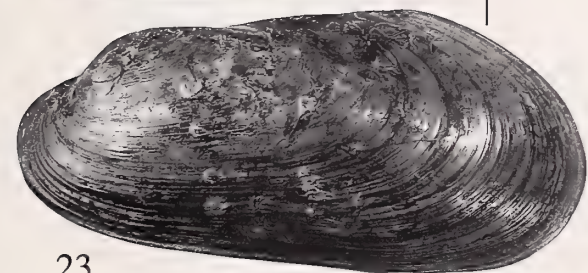
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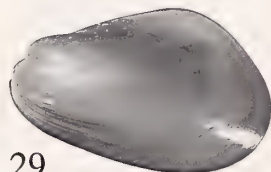
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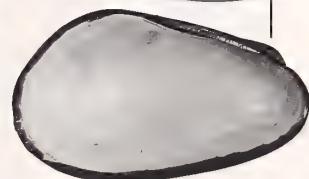
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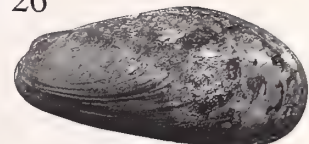
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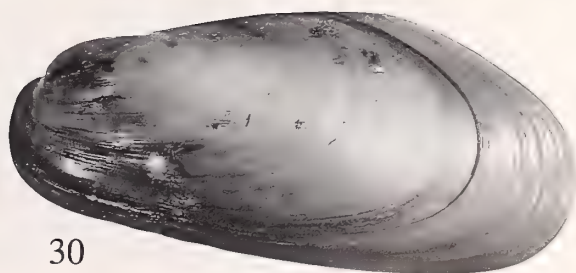
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nies of *Bathymodiolus azoricus* are more scattered, which could be due to the presence of soft substrate. Their temperature preferences are similar to those of the mussels at Lucky Strike, ranging from about 8°C (i.e., ambient seawater temperature) to about 30°C. The mussels derive their food from intracellular symbiotic chemoautotrophic bacteria, of both sulfide-oxidizing and methanotrophic types (Fiala-Médioni et al., 1996).

On Lucky Strike hydrothermal field, many specimens of *Bathymodiolus azoricus* harbor in their pallial cavity the commensal polynoid polychaete *Branchiopolynoe seepensis* Pettibone, 1986. This worm was found already in small individuals, from 33 mm length onward. In these small mussels, the polychaete is of course smaller but it can reach up to half the shell length. In the largest studied specimen of 119.3 mm, the worm was 45 mm long. In the Menez Gwen mytilids, *Branchiopolynoe* were never found. A detailed ecological description of the Lucky Strike vent field is given by Van Dover et al. (1996).

Distribution: *Bathymodiolus azoricus* is only known from the Menez Gwen and Lucky Strike hydrothermal fields on the Azores Triple Junction, Mid-Atlantic Ridge.

Etymology: The name expresses the proximity of the localities of this species to the Azores archipelago.

Remarks: *Bathymodiolus azoricus* shows an extreme variability, especially in shell shape, tumidity, and length/height ratio, but also in the position of the anterior scar of the posterior byssus retractor muscle, the form of posterior end of the ligament (ending abruptly or tapering), the thickness of the shell, the anterior and posterior mantle fusion, and the size of the labial palps.

The variability of the shell is so that two “extreme” specimens of *B. azoricus* suggest two totally different species. The general shell outline can be elongate-triangular to oval-oblong or even oval-elongate, almost date-shaped. The anterior margin may be broadly or rather narrowly rounded; the postero-dorsal corner is narrowly rounded to nearly indistinct and more or less integrated into the rounded posterior margin; the postero-dorsal mar-

gin is straight to convex. Growth allometry is also variable. The surface of the shells varies from smooth and quite glossy with relatively few growth lines to more or less covered with an oxide layer and numerous byssal endplates of other mussels, with strong and dense growth lines and somewhat coarser growth stages. The ventral pallial line is straight to rather markedly curved, this mostly (not always) when the ventral margin is also concave. The shell tumidity is also considerably variable (see Figures 12 and 14); extreme forms may be even more tumid than the maximum height of the shell.

This variability in shell shape and outline is present already in medium-sized and small specimens (see Figures 25–28); the latter often have a markedly convex ventral margin or in some specimens, the margin may be already somewhat concave. Specimens from some localities are small but have a more or less adult appearance with broad (high) shell, numerous well-marked growth stages, and oxide layer.

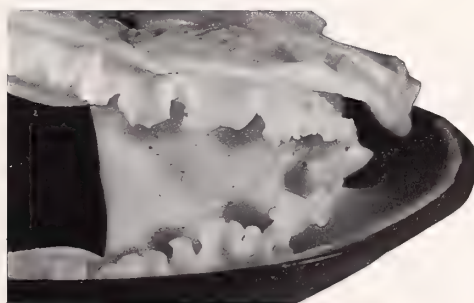
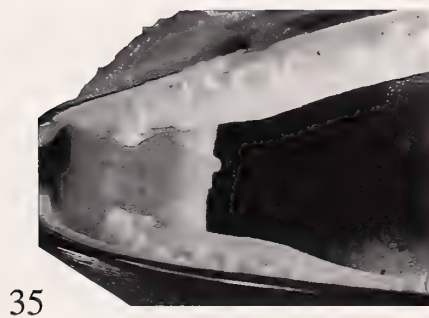
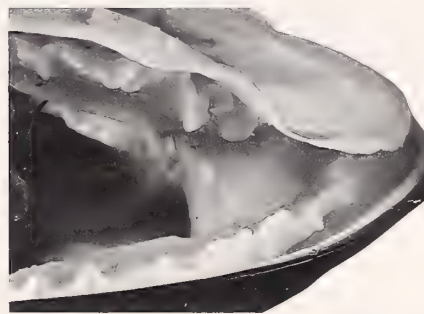
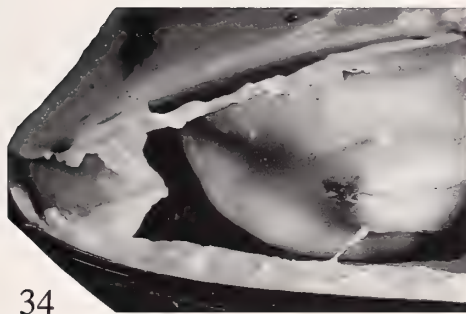
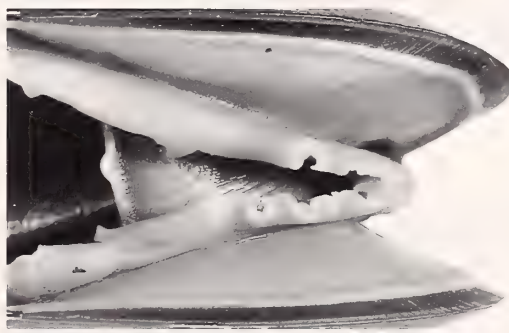
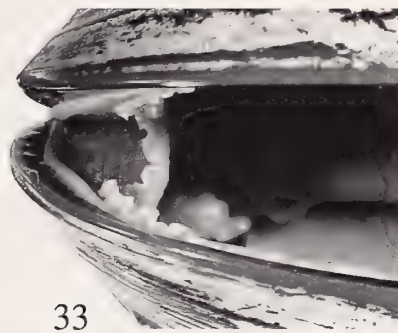
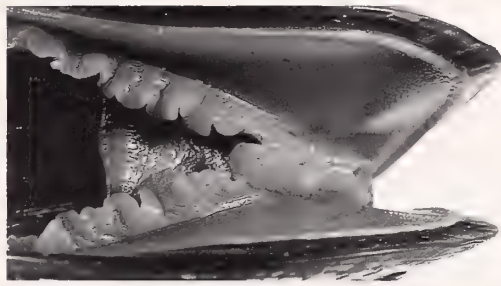
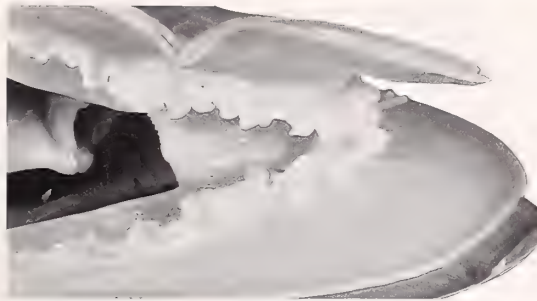
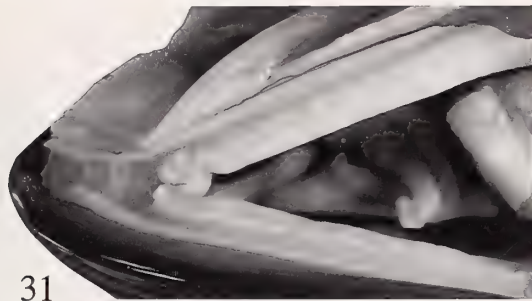
Gonads were already present in several specimens of 30–40 mm size; the smallest specimen with clearly visible gonads measures 31.8 × 16.5 mm and is from Menez Gwen; very few gonads were evident in a specimen of 25.4 × 16.5 mm from Isabel site (Lucky Strike) and one of 28.5 × 14.6 from Menez Gwen. Many of the small specimens with gonads are more or less thick-shelled and broad with many growth marks, but not in all cases; the above-mentioned 31.8 mm specimen is smooth, rather narrow, and quite thin-shelled. A few of the larger specimens (between 60 and 76 mm) were found with very few gonads or none at all; they all have a rather thin shell. One might expect gonads in the small forms with dense growth rings and thicker shell, which can be viewed as dwarf adults that grew more slowly under less favorable ecological conditions, but the presence of gonads in small, smooth, and thin-shelled juvenile-looking specimens from Menez Gwen still needs an explanation.

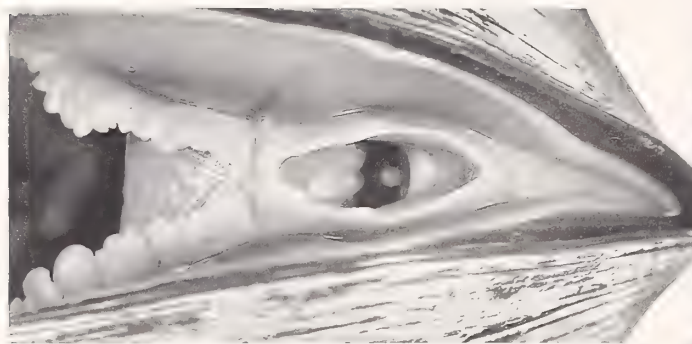
The soft parts also are variable: the papilla on the valvular siphonal membrane varies from being hardly visible as a slight curve only, to being large and strongly pro-

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Explanation of Figures 31–35

Figures 31–33. *Bathymodiolus azoricus* Cosel & Comtet sp. nov. Figure 31. Specimen from Menez Gwen hydrothermal field, site Mogued Gwen (same specimen as on Figure 30). Close-up view of anterior and posterior mantle fusion and posterior valvular siphonal membrane. Figure 32. Specimen from Lucky Strike hydrothermal field, site Pagoda (PP7), 37°17.63'N, 32°16.96'W, 1629 m, DIVA 2, dive 07, shell length 56.7 mm. Close-up view of anterior and posterior mantle fusion and posterior valvular siphonal membrane. Figure 33. Specimen from Lucky Strike hydrothermal field, same locality, shell length 59.3 mm. Close-up view of anterior and posterior mantle fusion and posterior valvular siphonal membrane. Note the different width of the “turning back” part above the anterior adductor in the three specimens. Figures 34, 35. *Bathymodiolus* sp. Figure 34. Specimen from Logatchev hydrothermal field, Irina site 14°45.10'N, 44°48.60'W, 3040 m, MIKROSMOKE, dive 21, shell length 69.1 mm. Close-up view of anterior and posterior mantle fusion and posterior valvular siphonal membrane. Figure 35. Specimen from Logatchev hydrothermal field, Irina site 14°45.10'N, 44°48.60'W, 3040 m, MIKROSMOKE, dive 21, shell length 71.6 mm. Close-up view of anterior and posterior mantle fusion and posterior valvular siphonal membrane.





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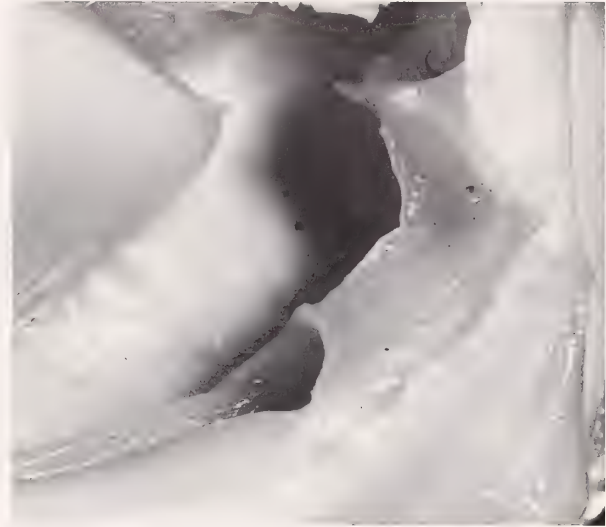
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Explanation of Figures 36–42

Figures 36, 37. *Bathymodiolus azoricus* Cosel & Comtet, sp. nov. Figure 36. Specimen from Menez Gwen hydrothermal field, site Mogued Gwen (PP10) 37°50.56'N, 31°31.27'W, 877 m, DIVA 2, dive 12, MNHN, 85.0 mm. Ventral view showing ventral opening. One valve removed. Figure 37. Specimen from Lucky Strike hydrothermal field, site Pagoda (PP7), 37°17.63'N, 32°16.96'W, 1629 m, DIVA 2, dive 07, MNHN, 59.3 mm. Ventral view showing ventral opening. Figure 38. *Bathymodiolus* sp.. Specimen from Logatchev hydrothermal field, Irina site 14°45.10'N, 44°48.60'W, 3040 m, MIKROSMOKE, dive 20, MNHN, 81.7 mm. Ventral view showing ventral opening. One valve removed. Figures 39–42. *Bathymodiolus azoricus* Cosel & Comtet, sp. nov. Figure 39. Specimen from Lucky Strike hydrothermal field, same locality, shell length 57.5 mm. Close-up view of exhalant siphon with clearly visible anal papilla. Figure 40. Specimen from Lucky Strike hydrothermal field, site Pagoda (PP7), 37°17.63'N, 32°16.96'W, 1629 m, DIVA 2, dive 07, shell length 56.7 mm. Close-up view of exhalant siphon. Figure 41. Specimen from Menez Gwen hydrothermal field, paratype, MNHN, shell length 107.8 mm. Detail of labial palps. Figure 42. Specimen from Menez Gwen hydrothermal field, paratype, MNHN, shell length 103.0 mm. Detail of labial palps.



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Explanation of Figures 43 and 44

Figures 43, 44. *Bathymodiolus azoricus* Cosel & Comtet, sp. nov., Specimen from Menez Gwen hydrothermal field, site Mogued Gwen (PP10) 37°50.56'N, 31°31.27'W, 877 m, DIVA 1, dive 13, sample 13.6. Shell length 81.1 mm. View into the siphonal cavity under two different angles. Note the anal papilla and the two tentacles on the lower transversal membrane directly under the siphonal opening (excurrent chamber) and on Figure 44 the posterior part of the incurrent chamber.

tuberant. Also the passage of the mantle edge over the anterior adductor from one valve to the other is rather variable (Figures 31–33).

All these highly variable characters are combined in nearly every sense, even within lots from the same site or dive, so that a clear delimitation of certain “morphs” is often not possible. However, in some sites, a tendency toward a certain form can be observed, especially in the site Statue of Liberty, where the specimens are exceptionally slender for a Lucky Strike population (Figures 6, 7).

Differences are more clear and seem to be more stable between the specimens of the two hydrothermal fields, Lucky Strike and Menez Gwen, which have a horizontal distance of about 60 km and a depth difference of about 800 m. Menez Gwen mussels have the umbos still somewhat more forward (see Figures 1–5) than those from Lucky Strike (for more details, see Biometry).

This variability is probably mainly due to abiotic ecological factors such as degree of nutrition (availability of nutrients), degree of venting activity (which can change rapidly), physico-chemical conditions, composition and temperature of the water, etc., but also to biotic factors, e.g., population density and competition. All these factors determine growth speed and growth allometry. The more tumid specimens with dense growth lines certainly did not have as favorable conditions as those with a smooth

surface, sharp margins, and no incrustations. These specimens obviously grew faster and were less disturbed. Some characters might perhaps also be related to genetic factors. In some sites (e.g., Menez Gwen) there is a tendency toward a certain homogeneity, but also there a few specimens of other “morphs” were present in a sample. In other sites, however, all morphs occurred together.

Two rather stable characters, however, which distinguish the shells of *B. azoricus* from *B. puteoserpentis*, are the position of the anterior byssus retractor scar and the position of the umbos relative to shell length. In *B. puteoserpentis*, the anterior byssus retractor scar is situated on the anterior part of the umbonal cavity in front of the umbos, whereas in the new species, the byssus retractor inserts more posterior within the umbonal cavity, normally directly under the umbos. *B. azoricus* is generally somewhat more elongate, and the umbos are always placed more forward than in *B. puteoserpentis*, at one-tenth to one-twelfth of shell length or more as opposed to one-seventh in *B. puteoserpentis*. Among the known vent mussels, only *B. platifrons* Hashimoto & Okutani, 1994, has similar almost terminal umbos.

We conclude that all “morphs” belong to a single very variable species and that even genetic differences between the sites (if present) are too small to warrant separation.

Bathymodiolus sp. aff. *B. puteoserpentis*
(Figures 16–24, 34, 35, 38, 53–56, 61, 63–67)

Description: Shell large, up to 123 mm long, thin but rather solid, modioliform-oval, considerably variable in outline, inflated, equivalve. Juvenile specimens in general somewhat shorter and more oval than adults but also already quite variable. Beaks subterminal. Anterior margin rather broadly rounded; ventral margin straight to slightly convex, in large and fully grown specimens often slightly concave in middle. Postero-ventral margin broadly rounded, postero-dorsal margin slightly convex to almost straight; postero-dorsal corner rather broadly to very broadly rounded; ligament plate arched, often more in its anterior half. Exterior with well-developed and strong, irregular growth lines and growth waves, which are well reflected on inside. In juveniles and half-grown specimens, weak and fine radial sculpture mostly visible in middle part of ventral half of valve as rather dense, irregular radial wrinkles (see Figure 19); occasionally also faint, narrow radial lines or waves on posterior slope (see Figure 17). Some faint radial structure also visible on inside of valves within shell material but not sculpturally reflected on the internal surface like growth lines. Umbos broad, very flattened.

Shell without periostracum dull whitish; interior nacreous white.

Periostracum strong, brown with a slight tendency toward olive, in umbonal and postero-dorsal region lighter brown, somewhat glossy, with no periostracal hairs; however, byssal endplates of other specimens always scattered over whole valve.

Hinge edentulous, anterior hinge margin, however, slightly protruding toward ventral. Ligament opisthodontic, strong, extending over almost whole postero-dorsal margin to postero-dorsal corner. Subligamental shell ridge very faint from under umbos to middle of ligament, then becoming obsolete; under beaks visible only in ventral view and not in lateral view. Anterior adductor scar long-oval, arched, situated in front of umbo. Posterior adductor scar rounded-trapezoid, united with posterior scar of posterior foot and byssus retractor muscle. Anterior scar of same muscle separated and situated under ligament, at

slightly behind two-thirds of its length (Figure 19). In smaller specimens, this scar is more backward (Figure 22) and in very small (35 mm and smaller) mussels, it is situated just behind ligament's end. Anterior byssus retractor muscle scar on anterior part of umbonal cavity just in front of beaks, visible only in posterior and ventral view but not in lateral view of interior. Pallial line ventrally straight, in large specimens often slightly concave when ventral margin is also concave.

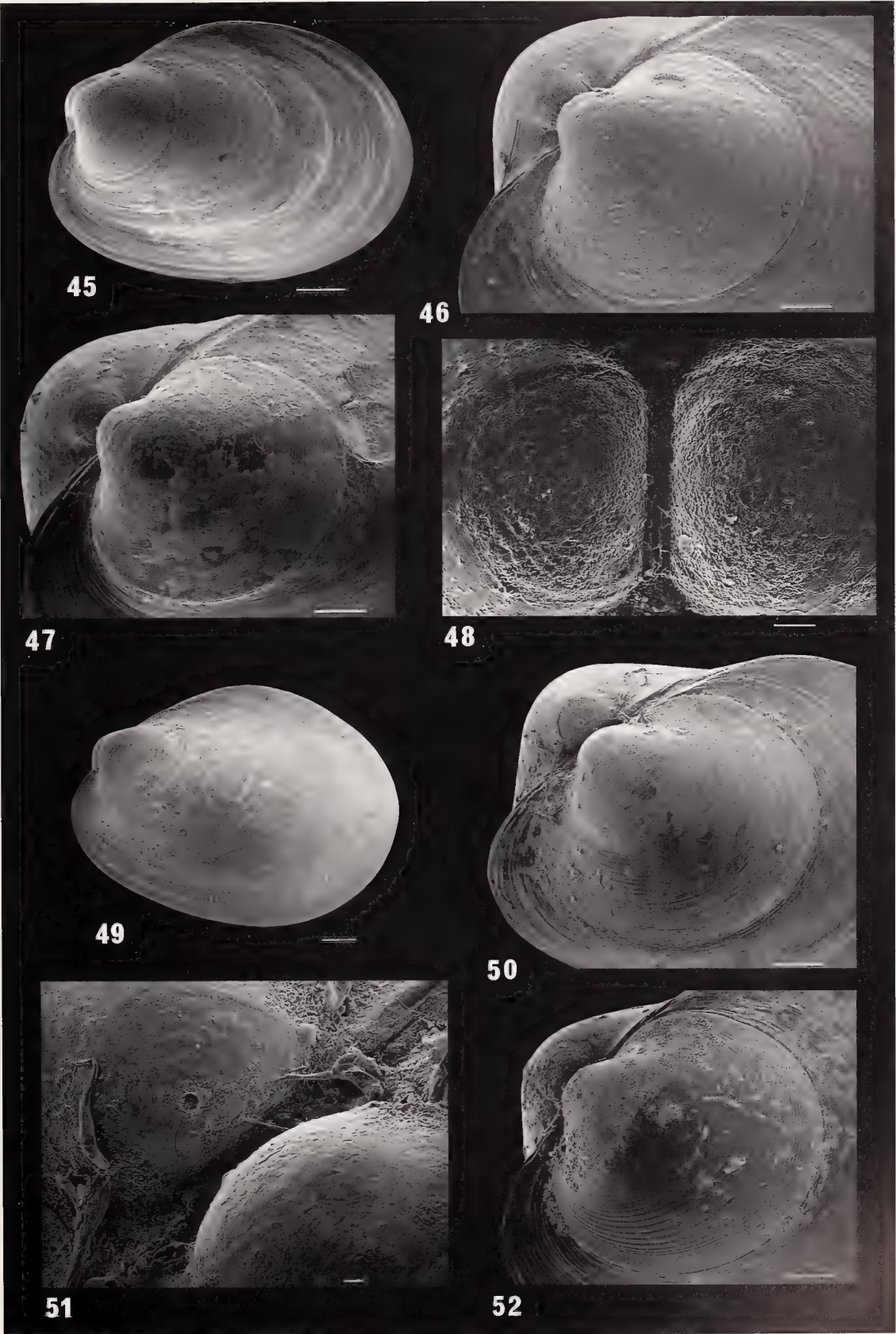
Larval shell 390–400 μm long and 380 μm high (Figures 53–56). Protoconch I 120 μm long, with irregular surface and well separated from Protoconch II, which indicates a long planktonic larval phase. Surface of Protoconch II with very fine, densely spaced and regular concentric grooves which may not always be visible.

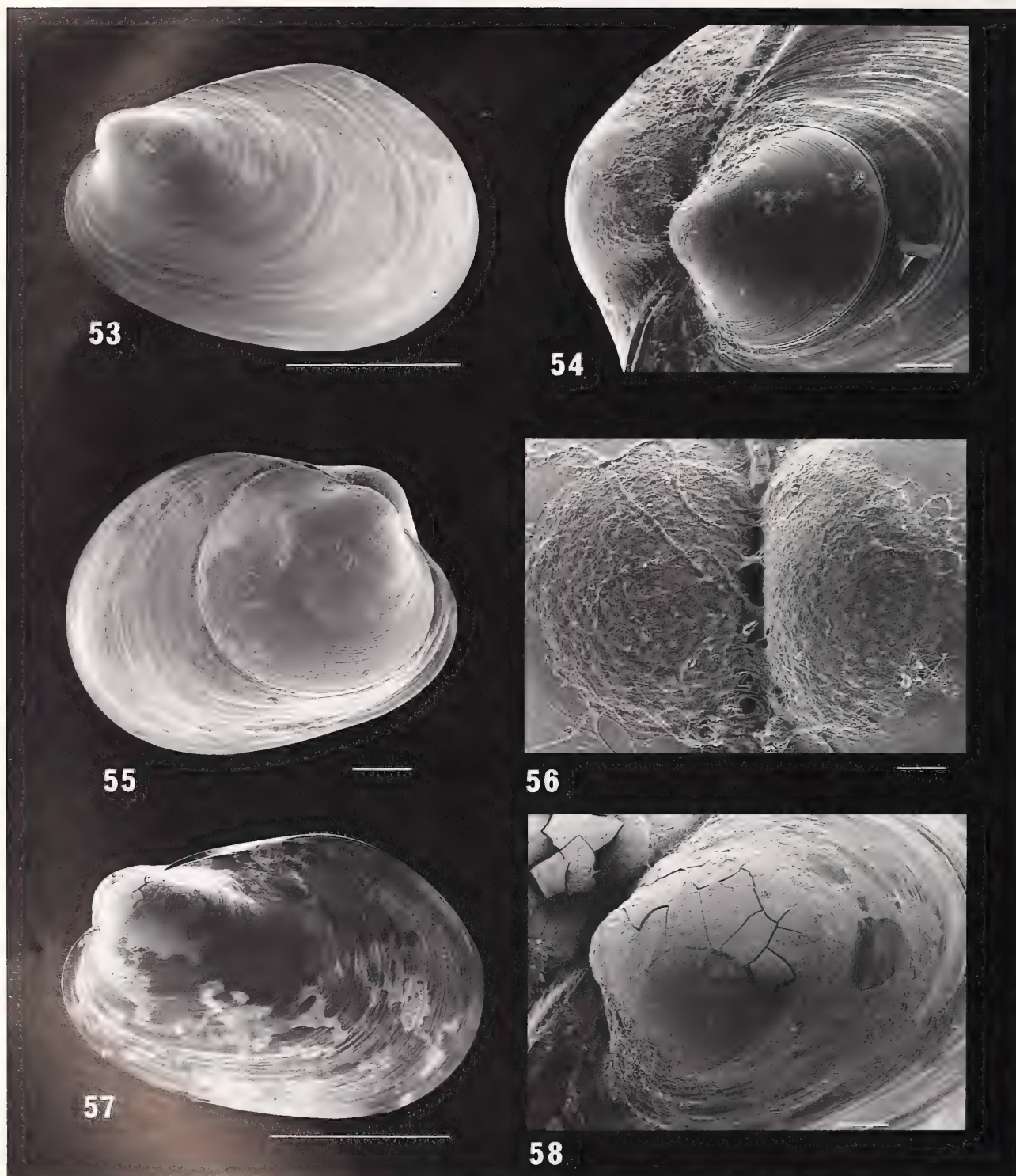
Animal with large ctenidia which are about three-fourths of shell length and cover entire visceral mass, each demibranch with descending and shorter ascending lamellae. Outer demibranch anteriorly slightly shorter than inner demibranch. Ascending lamellae of outer and inner demibranchs anteriorly fused to mantle and to visceral mass, respectively, for very short distance; more posteriorly gills entirely free from fusion. No muscular longitudinal ridges on mantle and visceral mass where dorsal edges of ascending lamellae attach. Connection bars between free edges and gill axes absent. Ventral edge with shallow food groove. Outer surface of ascending lamellae of both demibranchs with folds just below free edges and parallel to them. Filaments wide, fleshy, connected with each other by “plaquettes” and “racquets” (Le Pennec & Hily, 1984) on ventral and lateral sides, respectively. Approximately each fourth to seventh filament with septum reaching to half of gill height and connecting lamellae. In juvenile specimens, ascending lamellae of demibranchs much shorter than descending lamellae; in adult specimens, lamellae almost equal-sized.

Mantle thin, except for heavily thickened muscular margin and vascularized anterior region. Mantle edges with three folds; posteriorly, inner mantle folds fused dorsally above exhalent siphon and between exhalent siphon and combined inhalent aperture and pedal gape, forming short, narrow, and rather strong valvular siphonal mem-

Explanation of Figures 45–52

Figures 45–52. *Bathymodiolus azoricus* Cosel & Comtet, sp. nov. Larval shells. Figures 45–48. Specimens from Menez Gwen hydrothermal field, 37°50.54'N, 31°31.30'W, DIVA 2, dive 11. Figure 45. Juvenile specimen. Scale bar: 200 μm . Figure 46. Close-up view of Protoconch II of the same specimen. Scale bar: 100 μm . Figure 47. Protoconch II of another specimen. Scale bar: 100 μm . Figure 48. Protoconch I of another specimen. Scale bar: 20 μm . Figures 49–52. Specimens from Lucky Strike hydrothermal field, site Eiffel Tower, 37°17.32'N, 32°16.52'W, 1685 m, DIVA 2, dive 10. Figure 49. Juvenile specimen. Scale bar: 200 μm . Figure 50. Another specimen showing Protoconchs I and II. Scale bar: 100 μm . Figure 51. Close-up view of Protoconch I of the same specimen. Scale bar: 10 μm . Figure 52. Protoconch II of another specimen, showing the more or less widely spaced concentric striae. Scale bar: 100 μm .





Explanation of Figures 53–58

Figures 53–56. *Bathymodiolus* sp.. Specimens from Logatchev hydrothermal field, Irina site, 14°45.10'N, 44°48.60'W, 3063 m, MIKROSMOKE dive 20. Figure 53. Juvenile specimen. Scale bar: 1 mm. Figure 54. Close-up view of Protoconch II of the same specimen. Scale bar: 100 μ m. Figure 55. Ultra-juvenile specimen with well-distinguished Protoconch I and Protoconch II. Scale bar: 100 μ m. Figure 56. Close-up view of Protoconch I of the

brane which reaches from siphonal opening to postero-ventral corner and bears a small papilla. Anteriorly, inner mantle folds fused for very short distance underneath anterior adductor muscle. Mantle folds passing from ventrally over adductor muscle up- and forward along anterior margin, then folding down- and backward to pass again lower end of anterior adductor muscle toward ventral margin. Inner mantle folds frilled over all their length (Figure 38). Pallial muscles and siphonal retractors strong. Exhalent siphon short, inner aperture of it occluded by thin internal diaphragm with narrow horizontal slit. Muscular fold around slit which regulates aperture size. Two small, flattened tentacles directed toward anus situated under slit. As a branchial septum and a fusion of the gills with each other are absent, division of mantle cavity into a ventral incurrent and a dorsal excurrent chamber is not complete.

Foot thick, broad, flattened, tapering toward end, with ventral byssal groove three-fourths the length of foot. Anterior byssus retractor moderately long, strong, divided into three small blocks at about half its length. Posterior byssus retractor consisting of two strong, diverging muscle bundles of approximately equal width as anterior byssus retractor and having common base at base of byssus. Anterior bundle about two times shorter than posterior bundle and arising steeply toward attachment point on shell. Posterior bundle divided into two parallel bundles over all its length and passing at low angle to longitudinal shell axis. Posterior pedal retractor slightly more slender than other muscle bundles, arising from base of foot anterior to origin of posterior byssus retractors, passing outer side of anterior retractor toward anterior bundle of posterior byssus retractor. Posterior pedal retractors slightly asymmetrical, right one divided into two bundles at about half its length, both bundles inserting on inner and anterior sides of anterior bundles of posterior retractors. Left pedal retractor divided into two bundles over all its length, one bundle inserting on outer side of anterior bundle of posterior retractor at half its length, and other bundle inserting on inner side of anterior bundle.

Labial palps narrow, triangular, short but stout, strongly ridged on inner surfaces, anterior palps slightly smaller than posterior ones. Labial palp suspensor muscles present. From lateral sides of mouth between palps narrow fold running to base of gills. Labial palps of juveniles much shorter and sometimes lacking ridges.

Mouth transverse, slitlike, opening into short, thin-walled esophagus. Esophagus entrance at anterior end of stomach surrounded by dark digestive diverticula. Inner

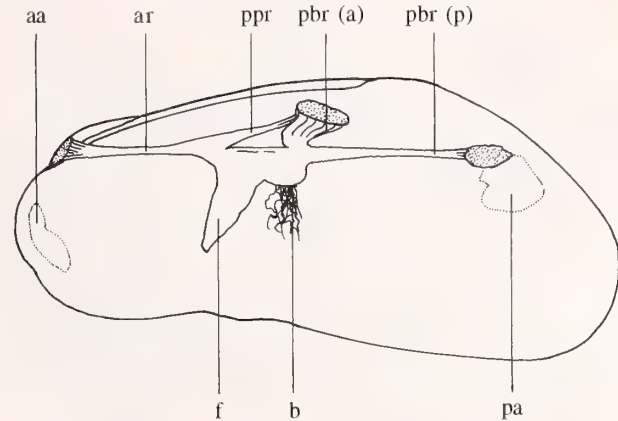


Figure 59

Sketch of foot-byssus retractor muscle complex of *Bathymodiolus azoricus* Cosel & Comtet, sp. nov., and its position in the shell (separate slender strand of anterior retractor serving as support for labial palps not drawn); specimen from Menez Gwen DIVA 2, Pl. 13; shell size 98.5 mm; aa, anterior adductor; ar, anterior retractor; ppr, posterior pedal retractor; pbr (a), posterior byssus retractor, anterior bundle; pbr (p), posterior byssus retractor, posterior bundle; pa, posterior adductor; f, foot; b, byssus.

surface of esophagus near its entrance into stomach bearing longitudinal ridges. Stomach (Figure 66) thin-walled, small, elongate, divided into a round anterior, and a more conspicuous posterior chamber. Major typhlosole arising from conjoined style sac and midgut, passing forward along floor of posterior chamber of stomach and terminating in shallow depression of floor of anterior chamber, possibly corresponding to food-sorting caecum. Gastric shield on antero-dorsal wall on left side of posterior chamber. Altogether, 11 ducts of digestive diverticula open into stomach. Posterior chamber with six openings. Three ducts of left side open into shallow depression below gastric shield, corresponding to left pouch. Small grooves leading from every opening of ducts and joining to form beginning of intestinal groove. Intestinal groove following major typhlosole, turning right and running along right side of major typhlosole into midgut. To right of intestinal groove and parallel to it, shallow groove running on lateral side of posterior chamber. Three ducts of digestive diverticula of right side opening along side of groove. Five ducts of digestive diverticula opening in anterior chamber near esophagus entrance—two openings from left side and three on floor and from right side. Crystal style present as amorphous mass. Arrangement of

same specimen. Scale bar: 20 μ m. Figures 57, 58. *Bathymodiolus puteoserpentis* Cosel, M  tivier & Hashimoto, 1994 (for comparison). Snake Pit hydrothermal field, Elan site, 23  22'N, 47  57'W, 3520 m, MIKROSMOKE dive 14. Figure 57. Juvenile specimen. Scale bar: 1 mm. Figure 58. Close-up view of Protoconch II, firmly covered by oxide layer but limits more or less visible. Scale bar: 100 μ m.

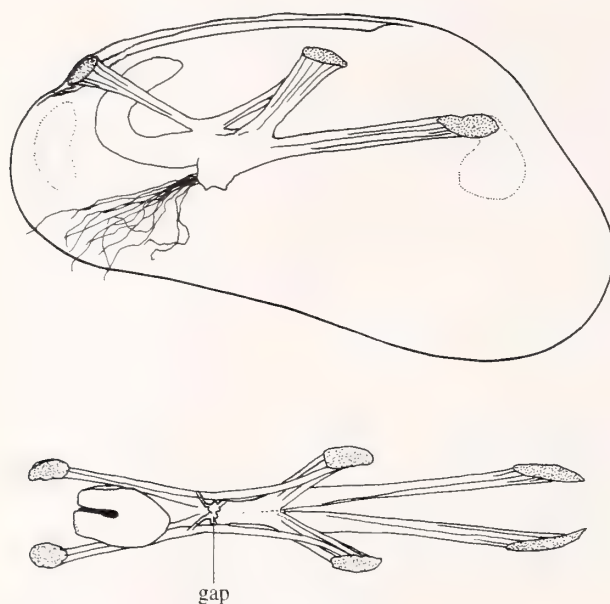


Figure 60

Sketch of foot-byssus retractor muscle complex of *Bathymodiolus azoricus* Cosel & Comtet, sp. nov.; specimen from Lucky Strike, DIVA 2, Pl 07, Pagoda. Shell illustrated on Figure 8, size 91.1 mm. Above, lateral view of the complex and its position in the shell (separate slender strand of anterior retractor serving as support for labial palps not drawn); below, ventral view (slightly enlarged as against the lateral view); gap, pedal ganglion.

openings of digestive diverticula to anterior stomach chamber may be variable. In very large specimens, inner surface of stomach more smooth and plain.

Midgut leaving the postero-ventral end of stomach and running for short distance posteriorly down mid-line, then entering pericardium and making very short counter-clockwise recurrent loop under ventricle before entering it ventrally and slightly anterior to auricular ostia. Rectum running directly down mid-line toward posterior and ending in a papillate anus on posterior surface of posterior adductor muscle. Dorsal wall of anus longer than its ventral wall, lateral sides bearing flattened ridges running to posterior point of attachment of gills axis to visceral mass. Shape of outgrowths of dorsal wall of anus variable. Examined stomach contained mytilid juveniles, sand, and mucuslike material; the rectum contained sand.

Heart three-chambered; ventricle rather large (in some preserved specimens), somewhat triangular, muscular, auricles very large, fused together posteriorly and with protrusions between bundles of posterior byssus retractors.

Kidney situated on each side of body below pericardium close to longitudinal vein, consisting of a thin-walled lobulate duct. Renopericardial apertures located in antero-lateral extremities of pericardium.

Sexes separate, gonads enclosing digestive diverticula and in large specimens extending into mantle. Genital ap-

ertures located at tips of small papillae in excurrent chambers near byssus.

Selected measurements (length, height, tumidity) with length-height ratios:

123.2 × 57.0 × 46.2 mm	Pl 21	2.2
120.7 × 54.4 × 46.6 mm	Pl 20	2.2
120.3 × 56.1 × 45.4 mm	Pl 21	2.1
94.7 × 49.6 × 39.8 mm	Pl 20	1.9
83.2 × 41.2 × 33.2 mm	Pl 21	2.0
81.9 × 39.8 × 31.1 mm	Pl 20	2.1
89.2 × 43.1 × 38.9 mm	<i>Akademik Mstislav Keldysch</i>	2.1
74.1 × 37.1 × 33.6 mm	<i>Prof. Logatchev</i>	2.0
72.7 × 36.7 × 30.7 mm	Pl 21	2.0
71.7 × 36.4 × 28.4 mm	Pl 20	2.0
71.4 × 38.4 × 30.6 mm	Pl 20	1.9
71.4 × 35.1 × 29.0 mm	Pl 20	2.0
68.0 × 33.4 × 31.4 mm	<i>Akademik Mstislav Keldysch</i>	2.0
69.3 × 35.7 × 32.2 mm	Pl 21	1.9
65.1 × 34.3 × 26.1 mm	Pl 21	1.9
61.5 × 32.5 × 27.3 mm	<i>Akademik Mstislav Keldysch</i>	1.9
54.5 × 30.6 × 23.7 mm	Pl 21	1.8
54.1 × 29.2 × 20.2 mm	Pl 20	1.9
53.5 × 31.2 × 24.7 mm	Pl 21	1.7
47.5 × 27.8 × 18.8 mm	Pl 20	1.7
41.2 × 24.2 × 15.2 mm	Pl 20	1.7
37.8 × 22.4 × 16.0 mm	Pl 20	1.7
31.7 × 19.4 × 13.2 mm	Pl 20	1.6
22.5 × 14.8 × 9.1 mm	<i>Akademik Mstislav Keldysch</i>	1.5
19.2 × 12.2 × 8.1 mm	<i>Akademik Mstislav Keldysch</i>	1.6
19.0 × 13.9 × 6.9 mm	<i>Akademik Mstislav Keldysch</i>	1.4
14.4 × 8.4 × 5.3 mm	<i>Akademik Mstislav Keldysch</i>	1.7
12.2 × 7.9 × 4.8 mm	<i>Akademik Mstislav Keldysch</i>	1.5
11.5 × 8.0 × 4.5 mm	<i>Akademik Mstislav Keldysch</i>	1.4
11.3 × 7.5 × 4.3 mm	<i>Akademik Mstislav Keldysch</i>	1.5
11.2 × 7.3 × 4.2 mm	<i>Akademik Mstislav Keldysch</i>	1.5
9.1 × 5.9 × 3.5 mm	<i>Akademik Mstislav Keldysch</i>	1.5
8.9 × 5.9 × 3.6 mm	<i>Akademik Mstislav Keldysch</i>	1.5
8.7 × 5.3 × 3.2 mm	<i>Akademik Mstislav Keldysch</i>	1.6
8.3 × 5.6 × 3.6 mm	<i>Akademik Mstislav Keldysch</i>	1.5

Material examined: Mid-Atlantic Ridge, 14°45'N, 44°58'W, Logachev hydrothermal field, cruise 35, R/V *Akademik Mstislav Keldysch*, sta. 3452, 16 spm. (among

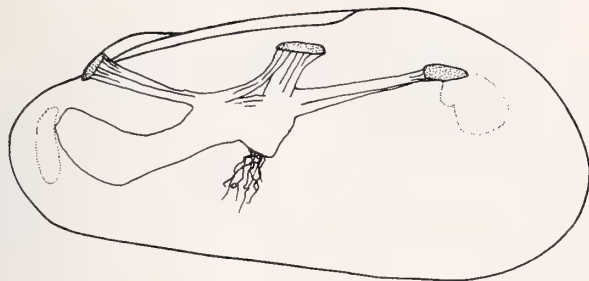


Figure 61

Sketch of foot-byssus retractor muscle complex of *Bathymodiulus* sp. from Logatchev and its position in the shell (separate slender strand of anterior retractor serving as support for labial palps not drawn); specimen from Pl. 21, shell length 120.3 mm. For explanation, see Figure 59.

them 12 juv.), 1 sh., taken by submersible Mir-2, dive 4/171, E.S. Chernjev, observer, 23 February 1995, ZMM Moscow. Irina site, 14°45', 10'N, 44°48.60'W, 3063 m, MICROSMOKE, dive 20, D. Prieur, observer, 5 December 1995, 11 spm., 20 juv. spm.; same locality, 3040 m, dive 21, Y. Fouquet, observer, 6 December 1995, 7 spm.; same locality, LOGATCHEV-7 cruise, R/V *Professor Lo-*

gatchev, 1 empty shell taken by TV equipped grab, July 1994, MNHN.

Biotope: The animal community of Logatchev hydrothermal field is dominated, in terms of biomass, by *Bathymodiulus* sp., which forms dense aggregations slightly below the zone of shimmering water (Gebruk et al., 1997). A commensal polynoid polychaete, which remains to be identified, was found in the mantle cavity of *Bathymodiulus* sp, but it occurs with a lower frequency than *Branchiopolynoe seepensis* in *Bathymodiulus azoricus*. In 23 examined specimens, only four were found to host the polychaete, and the worm was also smaller in relation to shell length than in *B. azoricus*. An ecological description of the Logatchev field is given in Gebruk et al. (1997).

Distribution: Mid-Atlantic Ridge, known only from the Logatchev hydrothermal field, 14°45'N, 44°58'W, 2930–3063 m.

Remarks: The mussels from the Logatchev field population are extremely close to *B. puteoserpentis*, and we do not find any really stable distinguishing character which would allow us to describe this *Bathymodiulus* as a new species separate from the Snake Pit mussels; however, there are some subtle differences in morphology

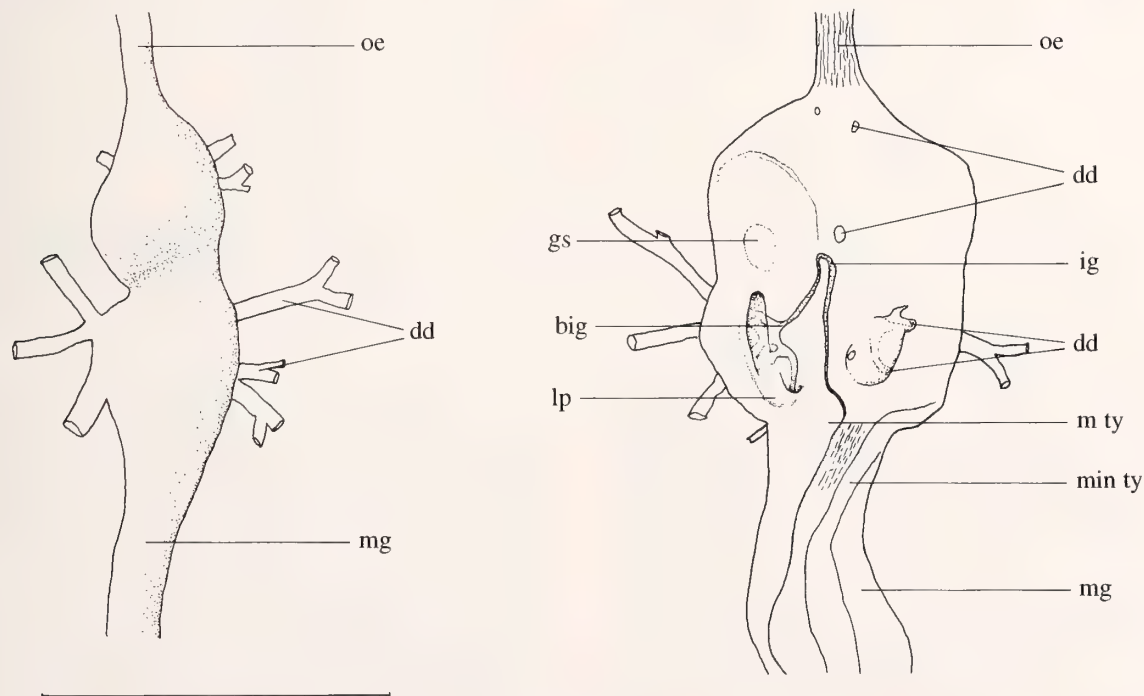


Figure 62

Stomach of *Bathymodiulus azoricus* Cosel & Comtet, sp. nov. from Lucky Strike. Half-schematic drawings from the same specimen as on Figure 60. Left, general view: above, anterior chamber; below, posterior chamber; dd, digestive diverticula ducts. Right, stomach opened dorsally; oe, esophagus; dd, digestive diverticula ducts (entrances); ig, intestinal groove; gs, gastric shield; big, beginning of intestinal groove; lp, left pouch; m ty, major typhlosole; min ty, minor typhlosole; mg, midgut. Scale: 1 cm.

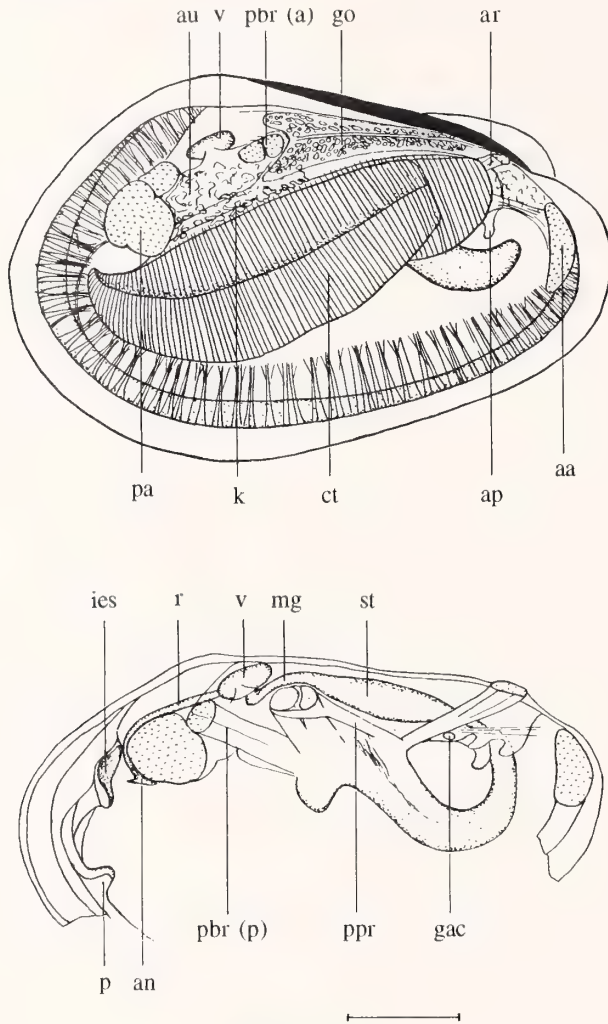


Figure 63

Bathymodiolus sp. Above, specimen of Figure 16, general view of soft parts. pa, posterior adductor; pbr (p), posterior byssus retractor, posterior bundle; pbr (a), posterior byssus retractor, anterior bundle; v, ventricle; au, auricle; go, gonads; k, kidney; ct, ctenidia; ar, anterior retractor; ap, anterior labial palps; aa, anterior adductor; f, foot. Below, another specimen, right mantle lobe and ctenidia removed. p, papilla of siphonal membrane; ies, inner aperture of exhalant siphon; r, rectum; mg, midgut; ppr, posterior pedal retractor; st, stomach; gac, cerebral ganglion. Scale: 1 cm.

(this paper) and genetics (Jollivet & Comtet, unpublished results). The mussel populations of both hydrothermal vent fields show a considerable variability in shell outline, and they overlap largely in their degree of variability. *Bathymodiolus* sp. differs from *B. puteoserpentis* from Snake Pit in its generally slightly thinner shell, which in very large specimens appears somewhat more elongate; however, in *B. puteoserpentis* rather elongate specimens were also found. The color of the periostracum tends more toward olive green in *Bathymodiolus* sp., and some

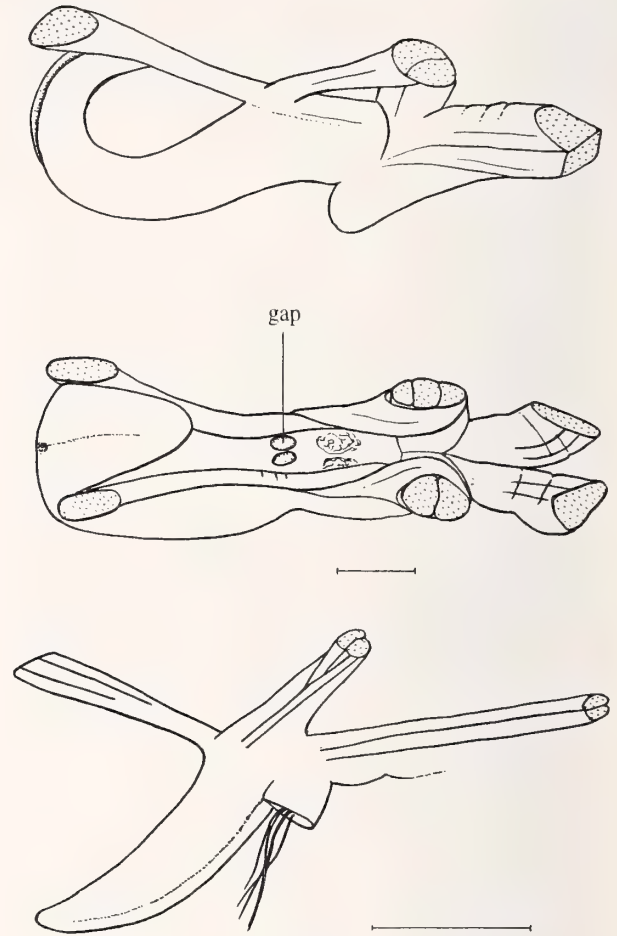


Figure 64

Bathymodiolus sp., foot-byssus retractor muscle complex. Above and middle: a juvenile specimen, lateral and dorsal view; below: holotype, lateral view; gap, pedal ganglion; for other explanations, see Figure 59. Scale: A-B: 1 mm; C: 1 cm.

specimens in coloration and surface with growth lines and growth waves, as well as in shell thickness, resemble freshwater mussels like *Anodonta*, whereas *B. puteoserpentis* is more chestnut brown. The irregular radial wrinkles on the middle part of the ventral slope are present in both species, but in *B. puteoserpentis* they are often less pronounced and also often hidden by the layer of oxide. The protoconch II in both populations is approximately the same size. The most important distinctive feature is the intestine, which in the observed *Bathymodiolus* sp. has a small counterclockwise recurrent loop under the ventricle, but in *B. puteoserpentis* the intestine changes its direction twice in an S-like manner in more or less the same plane. However, the shape of the intestine coiling seems to be variable within the same species or populations of both Snake Pit and Logatchev (and also in other species, unpublished observation in *B. brevior* Cosel, Mé-

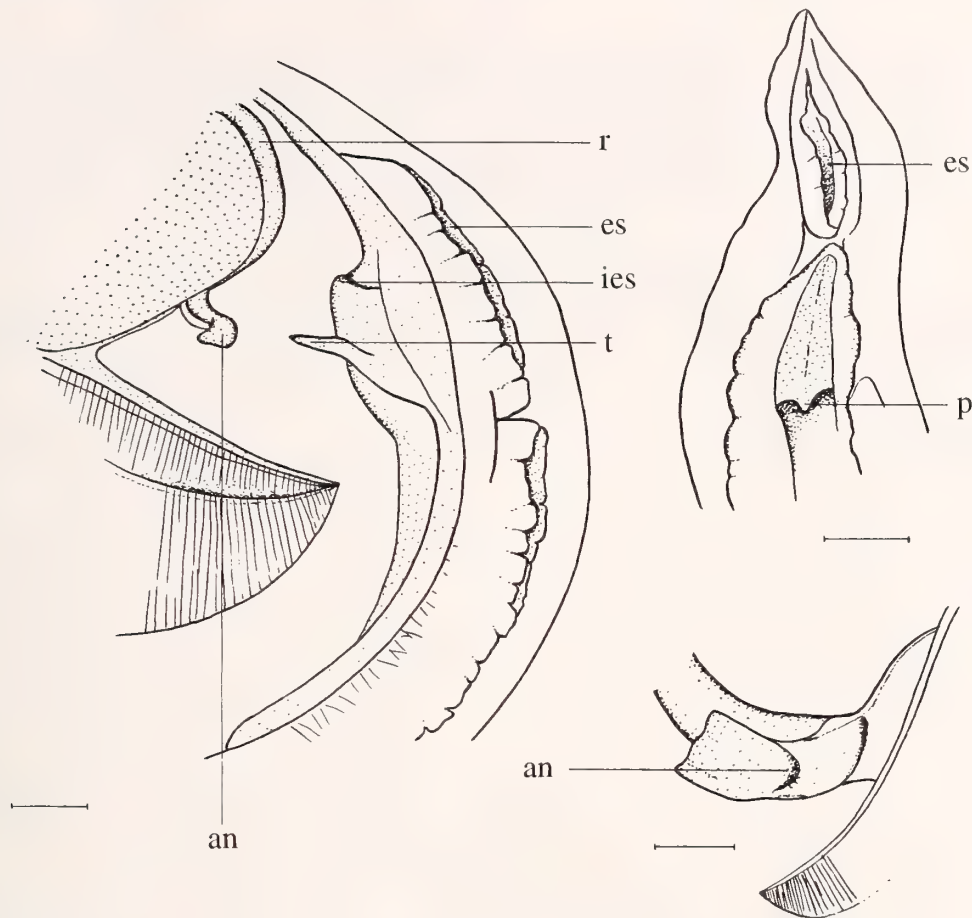


Figure 65

Bathymodiolus sp. Left, posterior part of soft parts, lateral view; upper right, exhalent siphon, posterior view; lower right, anus. r, rectum; an, anus; ies, inner aperture of exhalent siphon; es, exhalent siphon; p, papilla of siphonal membrane; t, tentacle of the lower transversal membrane. Scale: left: 2 mm; right: 1 mm.

tivier & Hashimoto, 1994), and with the few examined specimens of both populations at hand, we cannot for the moment use this character as the only one to separate the Logatchev population on species level. On the other hand, the slight morphological differences, as well as preliminary results of the current genetic research, do not permit us to identify the Logatchev mussel entirely with *B. puteoserpentis*.

Bathymodiolus azoricus is easily distinguished by the different shell outline, the almost terminal umbones with a very short anterior part, the considerably larger protoconch II, and the relationship of protoconch I/protoconch II. The protoconch I of *B. azoricus* is, in contrast to protoconch II, slightly smaller than in *Bathymodiolus* sp. A genetic study, which is currently in progress by the second author, will finally determine the genetic distances between the mussels from Logatchev, Snake Pit, and the Azores Triple Junction; these results and examination of

further material will also clarify the status of the Logatchev mussel.

Both *B. azoricus* and *Bathymodiolus* sp. are distinguished from *B. thermophilus* by the lack of a ventral mantle fusion, a more complicated stomach with left pouch, a coiled intestine, the absence of a lateral muscular ridge on the mantle lobes and visceral mass, and the absence of connecting bars between the free edges of the demibranchs and the gill axes. In comparison with *B. thermophilus*, the two species here treated are less specialized. They have a much closer affinity to other *Bathymodiolus*-like species from hydrothermal vents, e.g., *B. puteoserpentis* and an undescribed *Bathymodiolus* from the Mariana back-arc basin (Craddock et al., 1995). Apart from the intestine coiling, our two species do not differ from other vent *Bathymodiolus*-like mytilids in anatomical characters used by Craddock et al., 1995. See Table 1 for a comparison of features.

Table 1
Comparison of some features of *B. thermophilus* and MAR *Bathymodiolus*.

	<i>B. thermophilus</i> (from 13°N)	<i>B. azoricus</i>	<i>Bathymodiolus</i> sp. (Logatchev)	<i>B. puteoserpentis</i>
General shell form:	moderately elongate	more or less elongate	moderately elongate to stout	somewhat stout to moderately elongate
Tumidity:	more or less compressed	compressed to tumid	moderately tumid	moderately tumid
Shell:	thin but solid	thin to rather thick	thin but solid	thin but solid
Position of umbos:	subterminal	almost terminal	subterminal	subterminal
Position of anterior part of posterior byssus retractor muscle scar:	under the end of the ligament	under the end of ligament or more forward	at 2/3 of the ligament but variable	under posterior third of ligament, near the end
Position of anterior byssus retractor scar in the umbonal cavity:	slightly behind the umbos	under the umbos	under and in front of the umbos	under and in front of the umbos
Ventral pallial line:	markedly deflected	straight to deflected	straight	nearly straight
Intestine:	straight	counterclockwise loop	counterclockwise loop	changes direction twice
Mantle lobes on anterior half of ventral side:	fused	separate	separate	separate
Valvular siphonal membrane:	long and thin	short, narrow	short	short
Papilla in valv.s.memb:	present	present but variable	present, small	present
Muscular longitudinal ridge on mantle lobes and visceral mass:	present	absent	absent	absent
Posterior end of ligament:	tapering	abrupt to tapering	abrupt	abrupt to slightly tapering
Subligamental shell ridge:	strong and angular	obsolete from umbo to middle then missing	faint to obsolete	faint to obsolete

BIOMETRY

Length–Height Relationships

Figures 70 and 71 show the allometric relationships between shell height and length for the three species. Allometric curves were fitted following the allometric model of Teissier (1948), of the form $H = aL^b$, using Micro-soft Excel 5.0. For the three species treated, these curves indicate that length increases faster than height, traducing an elongation of the shell during growth. These results confirm those given by Comtet (1994) from samples collected on the sites Sintra and Eiffel Tower during the LUCKY STRIKE 93 cruise. For *Bathymodiolus azoricus* (Figure 70), the results indicate a great intersite variability in shell shape in individuals larger than 20 mm. The allometric relationship for the Menez Gwen population is in the range of those for Lucky Strike, indicating that mussels of both hydrothermal fields cannot be distinguished by biometrical characteristics. *Bathymodiolus* sp. and *B. puteoserpentis* have a similar shape in the observed length range (Figure 71).

For the statistical comparisons, length/height ratio was used as an index of shape (Cosel et al., 1994). Comparisons were made on individuals larger than 20 mm.

A one-way analysis of variance (ANOVA) was run to compare length/height ratios in *Bathymodiolus azoricus* from different sites of the Lucky Strike and Menez Gwen hydrothermal fields, in three different length classes (20–50 mm; 50–70 mm; larger than 70 mm) (Table 2). Due to the small sample size, the site PP5 was not included in the comparison. For the same reason, only four sites were considered for individuals larger than 70 mm. In each size class, length/height ratios are significantly different ($P = 0.0001$) (Table 2). However, pairwise comparisons using the Fisher PLSD test show no significant difference (significance level 95%) between the sites Isabel, Pagoda, and Sintra, in the three size classes.

	Fisher PLSD		
	20 ≤ L (mm)	50 ≤ L (mm)	70 ≤ L (mm)
	< 50	< 70	
Isabel vs. Pagoda	0.047	0.050	0.054
Isabel vs. Sintra	0.051	0.050	—
Pagoda vs. Sintra	0.041	0.049	—

All other pairwise comparisons show significant differences (significance level 95%).

Table 2

Bathymodiolus azoricus. Length/height ratios calculated for each site of the Menez Gwen and Lucky Strike vent fields, in three length classes. n: sample size.

	Mean	Standard	n	ANOVA
20 ≤ L (mm) < 50				
Isabel	1.756	0.136	45	P = 0.0001
Pagoda	1.781	0.120	108	
Eiffel Tower	1.833	0.147	535	
Sintra	1.763	0.133	67	
Statue of Liberty	2.051	0.130	592	
Menez Gwen	2.009	0.122	83	
50 ≤ L (mm) < 70				
Isabel	1.987	0.119	46	P = 0.0001
Pagoda	1.974	0.099	51	
Eiffel Tower	2.036	0.133	151	
Sintra	1.989	0.102	51	
Statue of Liberty	2.289	0.144	47	
Menez Gwen	2.162	0.126	114	
70 ≤ L (mm)				
Isabel	2.080	0.099	42	P = 0.0001
Pagoda	2.110	0.109	63	
Eiffel Tower	2.153	0.165	116	
Menez Gwen	2.286	0.130	89	

Table 3

Length/height ratios in *Bathymodiolus azoricus*, *Bathymodiolus* sp. (Logatchev) and *B. puteoserpentis* from different localities on the MAR, after the subsampling procedure. n: subsample size.

	Range	Mean	Standard	n
<i>Bathymodiolus azoricus</i>				
Eiffel Tower	1.387–2.619	2.057	0.201	100
Isabel	1.518–2.343	1.900	0.199	80
Pagoda	1.595–2.321	1.973	0.163	102
PP5	1.674–2.374	2.036	0.200	62
Sintra	1.491–2.419	1.909	0.199	74
Statue of Liberty	1.832–2.439	2.165	0.156	52
Menez Gwen	1.671–2.522	2.144	0.193	91
<i>Bathymodiolus</i>				
Logatchev	1.515–2.219	1.802	0.171	43
<i>Bathymodiolus</i>				
Snake Pit	1.624–2.087	1.930	0.127	19

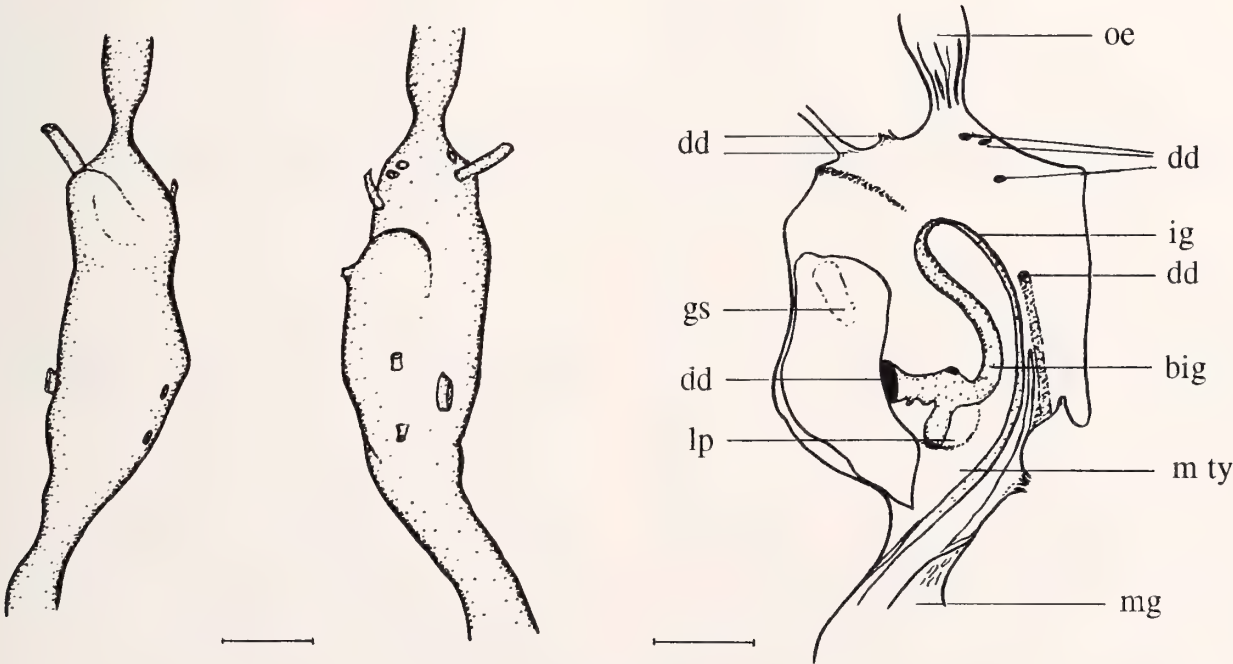


Figure 66

Bathymodiolus sp., stomach of specimen on Figure 16. Left: dorsal-lateral view; middle, ventral view; right, stomach opened dorsally. oe, esophagus; dd, digestive diverticula duct (entrance); ig, intestinal groove; mty, major typhlosole; gs, gastric shield; big, beginning of intestinal groove; lp, left pouch; mg, midgut. Scale: 2 mm.

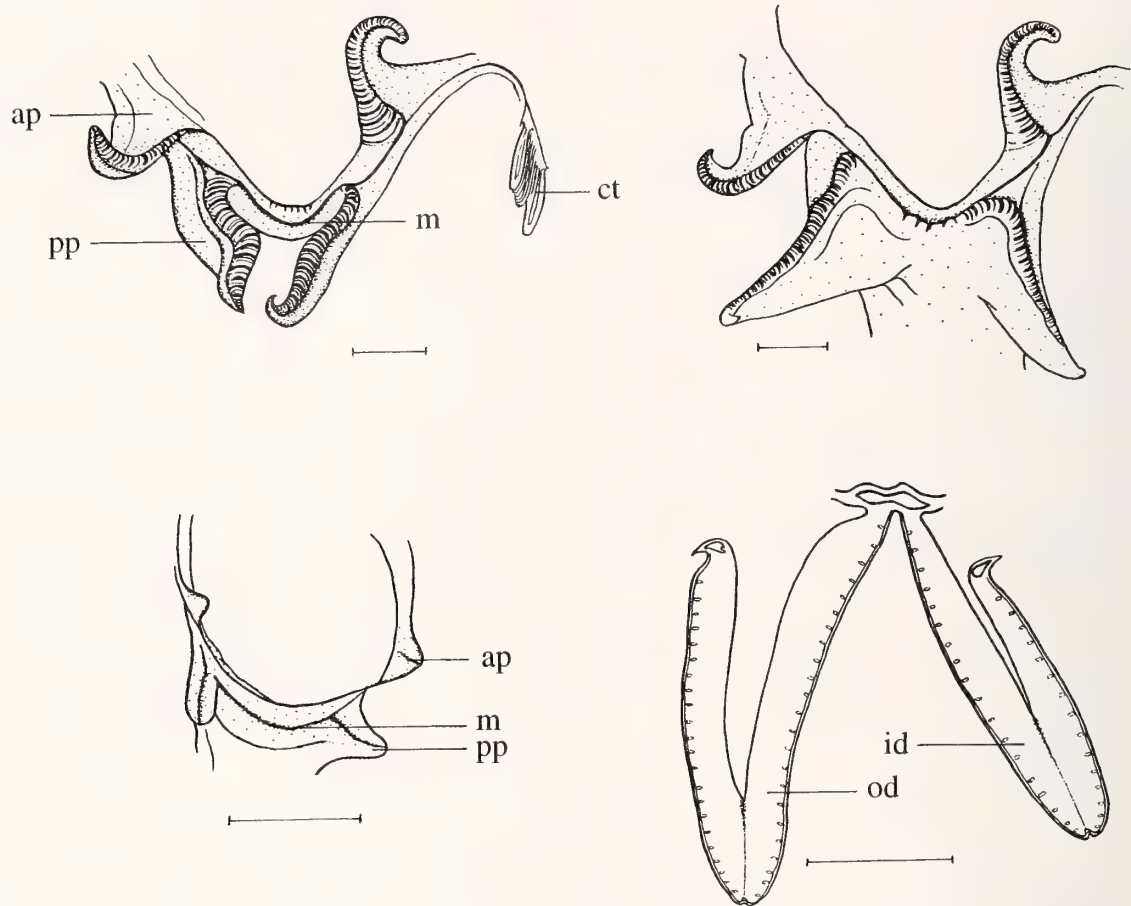


Figure 67

Bathymodiolus sp., upper row: labial palps of adult specimens, viewed from anterior end; below left: labial palps of juvenile specimens; below right: cross-section of ctenidia from the region anterior to pericardium; ap, anterior palps; pp, posterior palps; od, outer demibranch; id, inner demibranch; Scale: 2 mm; ctenidia: 1 mm.

A systematical subsampling procedure was realized by dividing the length range into 11 classes (20–30 mm; 110–120 mm; larger than 120 mm) and taking 10 individuals in each class when possible, in order to give the same weight to each size category. Table 3 gives length/height ratios calculated for each subsample (see also Figure 68).

Length/height ratios of *B. azoricus* and *Bathymodiolus* sp. were compared by means of a one-way ANOVA. Individuals of *B. puteoserpentis* from Snake Pit were not included in this comparison due to their low numbers. Length/height ratios are significantly different ($P = 0.0001$).

For *B. azoricus*, pairwise comparisons using the Fisher PLSD test show no significant differences (significance level 95%) between Isabel and Sintra, between Eiffel Tower and PP5, and between Statue of Liberty and Menez Gwen:

	Fisher PLSD
Isabel vs. Sintra	0.059
Eiffel Tower vs. PP5	0.060
Statue of Liberty vs. Menez Gwen	0.064

All other pairwise comparisons show significant differences at the 95% level. In particular, pairwise comparisons between each subsample of *B. azoricus* and the subsample of *Bathymodiolus* sp. from the Logatchev field indicate that length/height ratios in both species are significantly different at the 95% level.

Length/height ratios of *B. puteoserpentis* from Snake Pit and *Bathymodiolus* sp. from Logatchev are significantly different (Mann-Whitney U test, $P = 0.003$). However, if we consider only individuals larger than 50 mm in length (because the Snake Pit sample contains exclusively such large individuals), mean length/height ratios

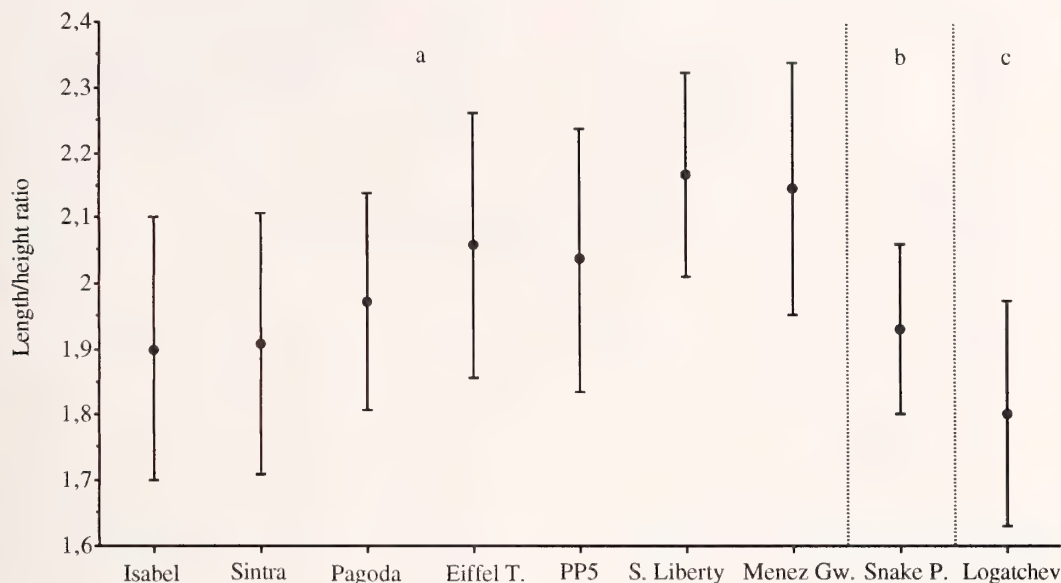


Figure 68

Length-height ratios of a. *Bathymodiolus azoricus* Cosel & Comtet, sp. nov. from different sites; b. *Bathymodiolus puteoserpentis* Cosel, Métivier & Hashimoto, 1994; c. *Bathymodiolus* sp. from Logatchev. Bars are 1 SD.

of *B. puteoserpentis* and *Bathymodiolus* sp. (respectively 1.930 ± 0.127 and 1.944 ± 0.140) do not differ significantly (Mann-Whitney U test, $P = 1$).

Anterior Part Length

Additional measurements of the anterior part length (i.e., the distance from the anterior margin to the umbo) were taken on 130 individuals of *Bathymodiolus azoricus* (75 specimens from Menez Gwen, 32 from Pagoda, and 23 from Eiffel Tower); 22 individuals of *Bathymodiolus* sp.; and seven individuals of *B. puteoserpentis*. Measure-

ments from Pagoda and Eiffel Tower were pooled and considered as representing *B. azoricus* from Lucky Strike. Total length/anterior part length ratios were then calculated and compared between the three species (Table 4 and Figure 69).

Bathymodiolus azoricus is clearly distinct from *Bathymodiolus* sp. and *B. puteoserpentis* with a total length/anterior part length ratio being two times higher for *B. azoricus*. Total length/anterior part length ratios in *B. azoricus* differ significantly between Lucky Strike and Menez Gwen (Student t test $P = 0.0004$), whereas in *Bath-*

Table 4

Total length/anterior part length ratios in *Bathymodiolus azoricus*, *Bathymodiolus* sp. and *B. puteoserpentis* from different localities of the MAR. n: sample size.

	Total length/anterior part length ratio			Total length range (mm)
	Mean	Standard deviation	n	
<i>B. azoricus</i>				
Menez Gwen	13.785	3.108	75	13.10–109.70
Lucky Strike	11.782	3.044	55	38.30–101.40
<i>Bathymodiolus</i> sp.				
Logatchev	6.610	0.936	22	36.90–123.40
<i>B. puteoserpentis</i>				
Snake Pit	7.250	0.799	7	98.20–136.10

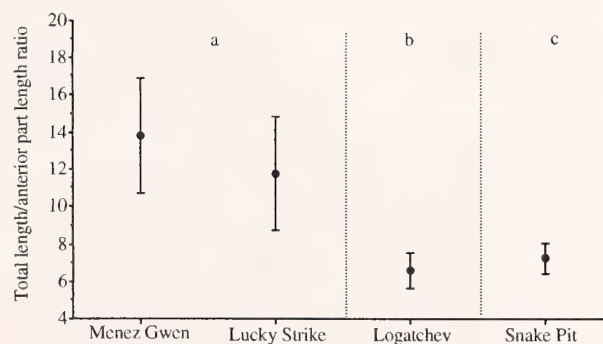


Figure 69

Ratios of total shell length/anterior part length of a. *Bathymodiolus azoricus* Cosel & Comtet, sp. nov. from Lucky Strike and Menez Gwen; b. *Bathymodiolus* sp. from Logatchev; c. *Bathymodiolus puteoserpentis* Cosel, Métivier & Hashimoto, 1994 from Snake Pit. Bars are 1 SD.

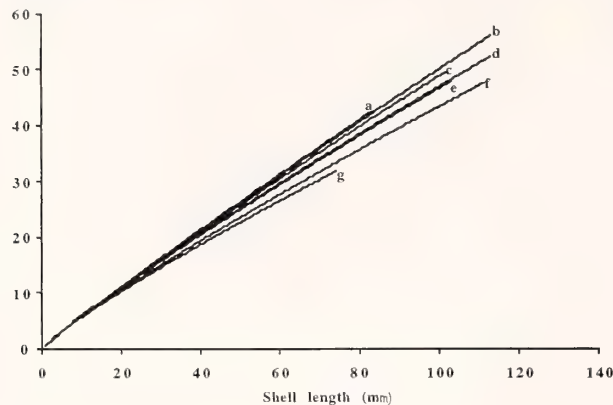


Figure 70

Shell height (H) vs. shell length (L) for *Bathymodiolus azoricus* from several sites of the Lucky Strike and Menez Gwen hydrothermal fields. Each curve represents the allometric model ($y = ax^b$) (Teissier, 1948) fitted to the observed data (not shown).

a Sintra	$H = 0.6838L^{0.9346}$	$r^2 = 0.9967$
b Isabel	$H = 0.6871L^{0.9317}$	$r^2 = 0.9968$
c Pagoda	$H = 0.7213L^{0.9158}$	$r^2 = 0.9954$
d Eiffel Tower	$H = 0.7671L^{0.8939}$	$r^2 = 0.9969$
e PP5	$H = 0.7504L^{0.8973}$	$r^2 = 0.9969$
f Menez Gwen	$H = 0.7724L^{0.8752}$	$r^2 = 0.9958$
g Statue of Liberty	$H = 0.7906L^{0.8592}$	$r^2 = 0.9967$

ymodiolus sp. and *B. puteoserpentis* they are significantly different at the 95% level but not at the 99% level (Mann-Whitney U test, $P = 0.0415$).

Remarks: The biometry study shows a great intersite (and interfield) variability of the shell shape in *Bathymodiolus azoricus*. However, from length/height ratio comparisons, three groups can be distinguished, corresponding to three different morphs: Isabel/Sintra, Eiffel Tower/PP5, and Statue of Liberty/Menez Gwen, the mussels from the latter being the most elongate (i.e., having the highest length/height ratio) (Figure 68). Specimens from Pagoda have a length/height ratio intermediate between the two first groups but can be associated with the first one (Isabel/Sintra). This variability is difficult to explain but could be due to intersite differences in the physico-chemical environment (temperature, fluid composition, etc.). Biotic factors such as mussel density could also affect the shell shape.

Despite such variability, *B. azoricus* of each site could be distinguished from *Bathymodiolus* sp. by the much higher length/height ratio, i.e., having a more elongate shell. The length/height ratio for *B. puteoserpentis*, intermediate between those of *B. azoricus* and *Bathymodiolus* sp., is not significantly different from that of *Bathymo-*

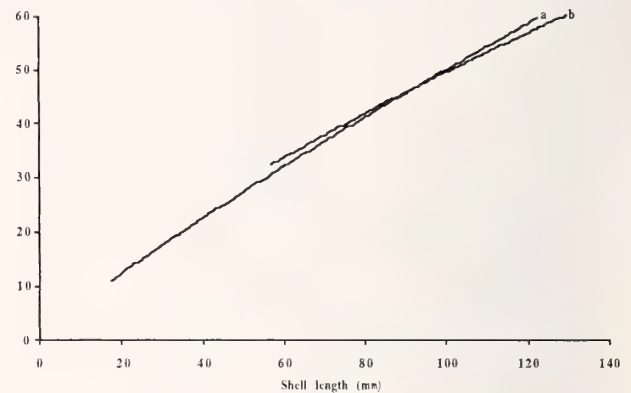


Figure 71

Shell height (H) vs. shell length (L) for *Bathymodiolus* sp. (a) from the Logatchev hydrothermal field and *Bathymodiolus puteoserpentis* (b) from the Snake Pit hydrothermal field. Each curve represents the allometric model ($y = ax^b$) (Teissier, 1948) fitted to the observed data (not shown).

a	$H = 0.9143L^{0.8679}$	$r^2 = 0.9928$
b	$H = 1.5232L^{0.7552}$	$r^2 = 0.9033$

diolus sp., when considering a similar length range (>50 mm).

Comparisons of the total length/anterior part length ratios confirm the morphological similarity between *B. puteoserpentis* and *Bathymodiolus* sp., whereas *B. azoricus* is well distinguished from these two species by the much shorter anterior part, i.e., by an almost terminal umbo (Figure 69).

DISCUSSION

From the study of the gross anatomy, it is evident that unlike the type species of the genus, *Bathymodiolus thermophilus*, all other large hydrothermal vent or cold seep mussels subsequently described under the generic name *Bathymodiolus* or still under study (Craddock et al., 1995; Cosel & Olu, 1998; Gustafson et al., 1998) have one major character complex which is distinct from *B. thermophilus*: the absence of an inner mantle fold fusion and the reduction of the valvular siphonal membrane to a short transverse sheet at the posterior end of the animal. In these mussels, the "ventral gape" stretches over the whole length of the shell, whereas in *B. thermophilus*, the fusion encloses the mantle cavity to a large extent, leaving only a rather small byssal and inhalant mantle opening. In connection with this, the other *Bathymodiolus* species lack a lateral muscular ridge on mantle lobes and visceral mass, and a posterior branchial septum, which in *B. thermophilus* divides more completely the excurrent and incurrent chambers. However, other "unusual" characters found by Kenk & Wilson (1985) in *B. thermophilus* (e.g., thick and very large ctenidia, very large auricles,

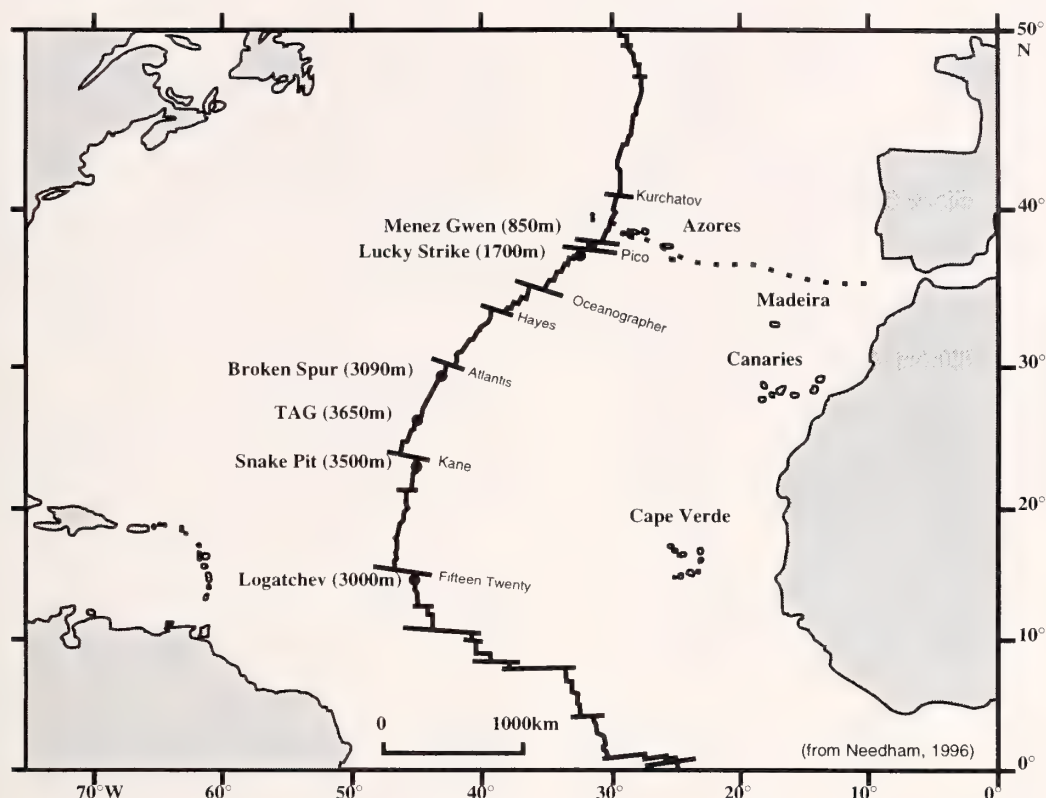


Figure 72

Map of the northern part of the Atlantic showing the known hydrothermal fields and transform faults on the MAR (taken from Needham, 1996).

symbiose with chemo-autotrophic bacteria) are present in the other species. The difference in the degree of mantle fusion, already discussed by Cosel et al. (1994), could lead to the introduction of a new genus to separate these species from *B. thermophilus*.

However, if one looks at Mytilidae of other genera of which the anatomy is described, none is known to have a similar ventral mantle fusion like *Bathymodiolus thermophilus*. This feature, only known from a hydrothermal vent mussel, has certainly developed after the separation of the *B. thermophilus* stock on the East Pacific Rise, and is a derived character, and only by chance, the most apomorphic species of the large mussels from hydrothermal vents was discovered and described first and is hence the name-bearer of the genus. Species without inner mantle fold fusion and very short valvular siphonal membrane are much more plesiomorphic in contrast to the apomorphic character of the fused inner mantle folds in the type species of the genus *Bathymodiolus*. A new supraspecific taxon cannot be introduced based on this.

Moreover, an electrophoretic analysis with 18 enzymes by Craddock et al. (1995) revealed a genetic distance *D* (Nei, 1978) of 1.865 between *Bathymodiolus thermophilus* and the Snake Pit mussel (now *B. puteoserpentis*) and

1.871 between *B. thermophilus* and the Lucky Strike mussel (now *B. azoricus*); the distance between *B. puteoserpentis* and *B. azoricus* is 1.179. The genetic distances (*D* values) between these three hydrothermal vent mussels are within the values usually found with species-level separation (Craddock et al., 1995).

Neither the morphological differences nor the genetic distance are a reason for introducing a new genus for the two species here treated, and as a consequence we maintain them in the genus *Bathymodiolus*.

Another difference, the more complicated stomach and the intestinal coiling in the species here treated versus the simple stomach without left pouch and with only three pairs of entering digestive gland ducts, and the straight digestive tract in *B. thermophilus* underlines that the latter is more apomorphic: it shows that the degree of direct filter feeding with digestion via the digestive tract has diminished in favor of nutrition by bacteria, whereas in our species, direct feeding remains more important.

Some Zoogeographic Remarks

Two species (and one population not recognized as full species) of *Bathymodiolus* associated with hydro-

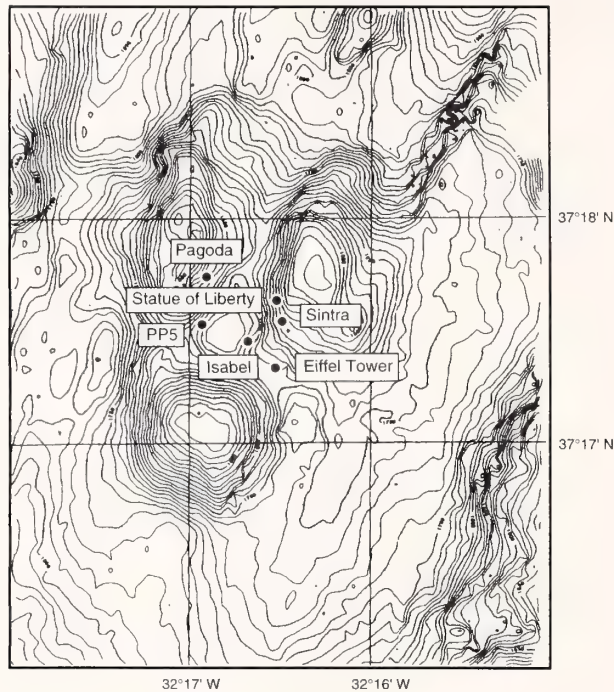


Figure 73

Map of the Lucky Strike hydrothermal field.

thermal activity are known to date from the MAR, but only a single species is found at one particular site. Their respective geographic range is limited to a few hydrothermal fields. The northernmost species is *B. azoricus*, which occurs at the Lucky Strike and Menez Gwen vent fields (37°17'N and 37°50'N, respectively). *B. puteoserpentis* inhabits the Snake Pit field (23°N), and *Bathymodiolus* sp. occurs on the Logatchev hydrothermal field (14°45'N). It was found that the morphological differences between the populations of Lucky Strike and Menez Gwen, on the one hand, and that of Snake Pit, on the other hand, are the most numerous and most obvious and have led us to distinguish two species. Differences between the Snake Pit population and the Logatchev population are less apparent but observable. Mussels from the Broken Spur hydrothermal field (29°10'N) are morphologically close to *B. puteoserpentis*, and were provisionally identified with this species by the first author. However, it is necessary to be cautious since the morphological analysis was conducted on only two broken shells. One specimen of a mytilid was collected on the TAG hydrothermal field (26°N, 3640–3680 m), but remains to be identified (P. Rona, personal communication). The endemism at specific level for the Mytilidae of the MAR was explained by a combination of depth effect and the role of transform faults on larval dispersal (Craddock et al., 1995; Van Dover, 1995; Van Dover et al., 1996).

The bathymetric ranges observed for each species indicate that the MAR mussels occupy two discrete bathymetric intervals. *B. azoricus* is restricted to shallower hydrothermal fields (850 m and 1700 m), whereas *B. puteoserpentis* and *Bathymodiolus* sp., as well as the mussels from Broken Spur and TAG, occur at depths exceeding 3000 m. The examination of ultrajuvvenile specimens and larvae in the Protoconch II stage from the Logatchev hydrothermal field showed that at least two different bivalve species are present, most probably the other also a mussel, so it is probable that another mytilid species reaches the site as planktonic larvae but does not find adequate conditions for settling.

Transform faults, which are numerous and various along the MAR (Needham, 1996), have been considered as barriers to the dispersal of vent invertebrates (e.g., Craddock et al., 1995; Van Dover, 1995; Van Dover et al., 1996) but their role may depend on the dispersal strategies of each species. Hydrothermal vent mytilids, and especially the species from the MAR, have a planktotrophic larval development, as inferred from size and morphology of the protoconch II (Lutz et al., 1980; Cosel et al., 1994; this paper), which allows the larvae to remain in the plankton for at least several weeks and to be widely dispersed by currents, after being driven by the plume to the level of lateral spreading several hundred meters above the bottom (Kim et al., 1994; Mullineaux & France, 1995; Mullineaux et al., 1995). One might expect that such a dispersal strategy would permit mytilid larvae to colonize vent fields separated by great distances regardless of transform faults or other physiographic features. Thus, the 45 km offset of the Pico transform fault (Figure 72), which separates Lucky Strike from Menez Gwen (with a distance of 60 km), does not constitute a major obstacle for the dispersal of *B. azoricus*. However, if the mussels from Broken Spur are clearly identified as *B. puteoserpentis* in the future, they would be the northernmost population of the species. The presence of three major faults (Oceanographer, Hayes, and Atlantis faults) between Lucky Strike and Broken Spur is a possible factor for differentiation between both areas. The Kane fracture zone, with an offset of 145 km, which separates Snake Pit and TAG/Broken Spur, does not seem to prevent dispersal of *B. puteoserpentis*, but the Fifteen-Twenty transform fault could explain reduced exchanges between Snake Pit and Logatchev. In addition to the possible role of transform faults, the low spatial frequency of occurrence of hydrothermal fields on the MAR, estimated at one field every 175 km by German et al. (1995), could limit the dispersal by lack of step-by-step processes. However, the occurrence of several other vent species (e.g., the alvinocaridid shrimp, *Chorocaris chacei* (Williams & Rona, 1986), the bythograeid crab, *Segonzacia mesatlantica* (Williams, 1988), the gastropod, *Protolira valvatoides* Warén & Bouchet, 1993, and the commensal polynoid

polychaete, *Branchiopolynoe seepensis*), with a wider geographical range on the MAR (Van Dover et al., 1996; Gebruk et al., 1997; Segonzac, personal communication), suggests that dispersal could occur along the entire MAR despite transform faults, and that these are not the only factors controlling the mytilid geographical distribution. Further investigations at intermediate depths and latitudes will allow us to precisely determine the role of depth and topography of the ridge in the distribution of mytilid species along the MAR.

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Note Added in Proof: After acceptance of this manuscript, two other papers with descriptions of mussels from hydrothermal vents and cold seeps were published: Cosel & Olu (1998) and Gustafson et al. (1998), which unfortunately could not be considered here. In total, six new species were described, among them four in the genus *Bathymodiolus*. This augments the total number of described and named species of hydrothermal vent and cold seep mussels to 13.

Shell Form and Color Variability in *Alia carinata* (Neogastropoda: Columbellidae)

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Abstract. *Alia carinata* from four different nearshore habitats in coastal central California were analyzed to investigate shell form and color variability. Analysis of select shell dimensions showed that *A. carinata* from an intertidal red alga, eelgrass, and benthic rock habitats displayed measurably and identifiably distinct forms. Individuals from giant kelp canopies showed considerable form overlap with benthic specimens, and likely represented benthic migrants. Interhabitat form variability was related to differences in both shape and size, while observed sexual dimorphism appeared to be strictly size-related, with males larger than females. *A. carinata* from eelgrass were mostly unpatterned and dark in color, while those from the other three habitats were generally patterned and variably colored. Planktonic dispersal of juveniles and the lack of discontinuous shell phenotypes suggest that observed interhabitat form variability was not a result of developmental polymorphism. Rather, phenotypic plasticity and post-settlement selection, potentially resulting from predation and wave exposure differences among sampled habitats, are suspected as important mechanisms in observed intraspecific shell form and color variability.

INTRODUCTION

Alia carinata (Hinds, 1844) are planktotrophic, determinate-growth gastropods which range from Forrester Island, Alaska, to southern Baja California (McLean, 1978, 1996). *Alia carinata* rarely exceed 11 mm in shell height, and are found commonly on intertidal rocks and algae, within the surfgrass *Phyllospadix* spp., and subtidally on kelp stipes and holdfasts (Abbott & Haderlie, 1980). Jones (1971) noted that *A. carinata* may sometimes be the most abundant animal living on the kelps *Macrocystis* spp. Densities of 110 individuals per 0.01 m² have been observed within an intertidal red algae habitat (Tupen, unpublished data).

At maturity, this species displays variable shell coloration, although most are some variation of a light to dark brown base color with fine to large markings or regular patterning (Crane, 1969; Carlton & Roth, 1975; McLean, 1978; Abbott & Haderlie, 1980; Carter & Behrens, 1980). Carter & Behrens (1980) referred to several color variants of *A. carinata*: a “common banded form” from the rocky subtidal; a patterned “open coast” form; and a “predominantly uniform dark brown to black” form collected from eelgrass (*Zostera marina* Linnaeus). Bergman et al. (1983) demonstrated that *A. carinata* from a sheltered harbor environment displayed highly developed shoulder keels, and large shell width to shell height ratios, relative to those collected from an exposed rocky cove.

Intraspecific shell color and pattern variability are well known in marine prosobranchs, e.g., Hughes & Mather, 1986, in *Littorina* sp. (Littorinidae); Etter, 1988, in *Nucella* sp. (Thaididae); Langan-Cranford & Pearse, 1995,

in *Lacuna* spp. (Lacunidae). Although intraspecific shell form variability is not uncommon in gastropods—e.g., Naylor & Begon, 1982, in *Littorina* sp.; Dillon, 1984, in *Goniobasis* sp. (Pleuroceridae); Tissot, 1984, in *Cypraea* sp. (Cypraeidae); Katoh & Foltz, 1994, in *Viviparus* sp. (Viviparidae)—the literature addressing the nature and extent of, or potential factors controlling, shell form variability in *A. carinata* is limited (i.e., Bergman et al., 1983).

The purpose of this study was to identify and describe intraspecific shell form and color variability among *Alia carinata* from four different habitats, and to generate hypotheses concerning the controlling factors and adaptive advantages of variable shell forms. This study was not specifically intended to characterize habitat-dependent forms, as this would have required a different study design. Results of this research demonstrated that: (1) both size- and shape-related distinct shell forms existed in three of four sampled habitats; (2) sexual dimorphism was size-related; and (3) shell pattern frequencies were habitat-dependent.

MATERIALS AND METHODS

Specimen Collection and Processing

Identifications of *Alia carinata* were based on shell descriptions in Carlton & Roth (1975) and McLean (1978). *Alia tuberosa* (Carpenter, 1864), the only local congener of *A. carinata*, are distinguished by their flattened whorls and smaller shell heights at maturity (Carlton & Roth, 1975; McLean, 1978). Approximately 75–100 individuals of *A. carinata* were collected off central California, from

Morro Bay (35°22'N, 120°52'W) south to Diablo Canyon (35°12'N, 120°51'W), San Luis Obispo County, from each of the following habitats and approximate tidal elevations: subtidal rocky benthic (−10 m mean lower low water, MLLW, hereafter abbreviated RB in text); intertidal *Gastroclonium subarticulatum* (Turner) Kützing (Rhodophyta, −0.3 m MLLW, hereafter abbreviated GS in text); shallow subtidal eelgrass blades (*Zostera marina*, −2 m MLLW, hereafter abbreviated ZM in text); and giant kelp (*Macrocystis pyrifera* (Linnaeus) Agardh, −1.3 m MLLW, hereafter abbreviated MP in text) canopy blades. The first three habitats were selected to represent those in which Carter & Behrens (1980) and Bergman et al. (1983) had noted characteristic *A. carinata* shell colors and forms. The habitat MP was selected because my qualitative observations suggested a habitat-specific shell color variant.

Most *A. carinata* were collected during the winter and spring of 1995 and 1996, except for specimens from GS, which were collected during the winter, spring, and summer of 1993 and 1994. Bias during collection in the MP and ZM habitats was minimized by indiscriminately scraping fronds and leaves, respectively, by hand into a collection jar. Specimens of *A. carinata* from GS were collected by completely scraping algae masses (0.01 m² patches, collected for a related project) from their rock substrates and later sorting *A. carinata* from the algae. Collection bias was less easily avoided in the RB habitat, as *A. carinata* often occurred in depressions and on irregular surfaces, which made indiscriminate sampling difficult. In this habitat, rocky substrate was examined closely and all *A. carinata* observed were collected.

Determination of shell patterning and form was sometimes prohibited by the presence of epizooic, non-geniculate coralline algae (Rhodophyta: Corallinaceae). The majority of *A. carinata* specimens from MP and ZM habitats were encrusted by coralline algae by the middle of each year (May–June), while earlier collections of *A. carinata* were rarely encrusted. Attempts at removing the algae by scraping with forceps proved difficult. Consequently, analysis of color and form in this study was restricted to non-encrusted specimens. In addition, only unbroken individuals were considered for analysis. These field samples therefore resulted in the collection of the following number of eligible, conchologically adult *A. carinata* (evidenced by a thickened and reflected aperture outer lip) from each of the following habitats: RB (n = 54); GS (n = 66); MP (n = 52); and ZM (n = 50). Fifteen male and 15 female unbroken individuals were randomly selected from each of these four groups for morphometric analysis. Male individuals were identified by the presence of the conspicuous penis.

Each snail was drawn with a camera lucida and dissecting microscope at 15×, using the position illustrated in Figure 1 and positioning methods described in Coppoisi & Glowacki (1983). The following six dimensions were

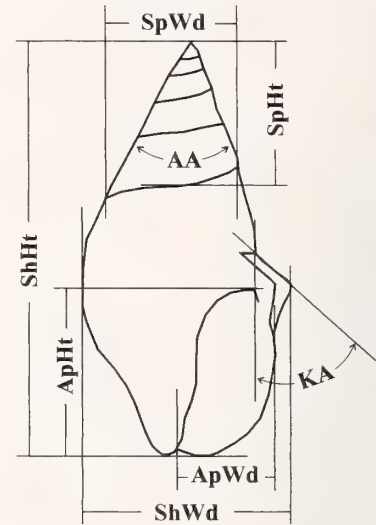


Figure 1

Alia carinata shell dimensions measured for morphometric analyses: ShHt, shell height; ShWd, shell width; SpHt, spire height; SpWd, spire width; ApHt, aperture height; ApWd, aperture width; AA, apical angle; KA, keel angle. See text for landmark descriptions.

measured from each magnified drawing using a slide caliper (instrument precision 0.1 mm): shell height (ShHt); shell width (ShWd); spire height (SpHt); spire width (SpWd); aperture height (ApHt); and aperture width (ApWd) (Figure 1). All of these dimensions were measured parallel or perpendicular to the central axis of the shell. ApWd did not include the shoulder keel, if present, but was landmarked laterally between the usable, functional aperture opening (Figure 1). SpWd was the widest dimension of the penultimate whorl. SpHt was landmarked between the apex and the body whorl suture at its intersection with the shell central axis. Caliper measurements of magnified drawings were converted to actual dimensions in millimeters referencing an actual shell height determined with a dial micrometer (instrument precision 0.025 mm). Apical angle (AA), in degrees, was calculated by computing the arc tangent of the SpWd: SpHt ratio. This dimension was calculated as an estimator of whorl expansion rate. The extent of shoulder carina (keel) development was quantified with the variable keel angle (KA), measured from the magnified drawing in degrees with a protractor (instrument precision 0.5°). The variable KA was defined as the angle formed between a vertical line drawn through the right marginal body whorl suture (vertex), and a line drawn from this vertex to the widest point of the aperture (Figure 1).

Distortion with the camera lucida potentially due to portraying three-dimensional objects in two-dimensional space was minimized by using the same microscope at the same magnification for conchological adults identi-

Table 1

Alia carinata shell variables used in the morphometric analyses. Values reported were obtained by repeated measurements ($n = 10$) on the same individual, see text for methods. Apical and keel angle in degrees, all other dimensions in mm.

Variable	Symbol	Mean	SD	Min	Max
Shell height	ShHt	7.96	0.07	7.9	8.1
Shell width	ShWd	4.12	0.05	4.0	4.2
Spire height	SpHt	2.77	0.05	2.7	2.9
Spire width	SpWd	2.34	0.02	2.3	2.4
Aperture height	ApHt	3.33	0.04	3.3	3.4
Aperture width	ApWd	1.53	0.05	1.4	1.6
Apical angle	AA	40.18	0.44	39.5	40.9
Keel angle	KA	51.70	1.09	50.0	53.0

cally positioned in the center of the field of view. Measurement error was estimated by drawing one test individual with the camera lucida on 10 separate occasions, removing it from, and repositioning it on, the stage after each drawing. The means, standard deviations, minimums, and maximums from these repetitions are presented in Table 1. This exercise demonstrated that the methods used in this study provided repeatable and accurate estimations of most shell variables measured. The variable KA was sensitive to slight differences in positioning on the microscope stage, and this was reflected by its relatively low precision ($SD = 1.09^\circ$).

Data Screening

Although MANOVA and ANOVA are robust to deviations from normality and variance homogeneity if sample sizes are fairly large and equal among groups (Pimentel, 1979; Zar, 1996), the presence of univariate or multivariate outliers can cause serious deviations from these assumptions and lead to results that distort statistics and do not generalize to the population(s) being sampled (Tabachnick & Fidell, 1996; Zar, 1996). Univariate outliers, by habitat and sex, were identified by comparing standardized (z -score) variable values against a critical score of 3.29 at $\alpha = 0.001$ (2-tailed). Multivariate outliers, by habitat and sex, were identified by inspecting Mahalanobis distances (D^2), evaluated against a critical χ^2 value of 26.12 at $\alpha = 0.001$, with 8 degrees of freedom (corresponding to the number of variables). Tabachnick & Fidell (1996) recommended that both of these outlier screening procedures be evaluated at a very conservative $\alpha = 0.001$.

Interhabitat Shell Form

Univariate size and shape differences among habitats were examined using ANOVA and ANCOVA. Prior to ANCOVA, dependent variables, by habitat, were first

tested for significant linear relationships with the covariate, and then tested to ensure homogeneity of slopes among groups. The ratio ShWd:ShHt was analyzed with ANOVA to provide comparative data for the only quantitative reference on *A. carinata* shell form variability to date (Bergman et al., 1983). Shoulder keel development, using a rating scale (1 to 5, where 1 represented least keeled, and 5 represented most keeled) presented in Bergman et al. (1983), was analyzed using a Kruskal-Wallis non-parametric ANOVA (H-statistic). Unplanned pairwise comparisons following significant ANOVA results were Student's t -tests for the parametric case, and Tukey-type Nemenyi tests (q -statistic) for the non-parametric case (Zar, 1996). Bonferroni adjustments were made to the calculated comparison-wise error rates to protect against Type I error rate inflation. The experiment-wise error rate was maintained at $\alpha = 0.05$ for all analyses in this study unless noted otherwise.

MANOVA was used to test for among-group population centroid differences using the eight variables from this study. The two variables analyzed in Bergman et al. (1983)—the ordinal scale keel development rating, and the ratio ShWd:ShHt—are arguably and conditionally inappropriate for multivariate analyses (Pimentel, 1979; Tabachnick & Fidell, 1996), and were not included in the MANOVA. If a significant difference existed among groups, canonical variate analysis (CVA) was used to interpret these differences. A forward selection, F-to-enter, stepwise CVA procedure was used to determine which subset of the eight variables was optimal in separating group forms. An optimal subset was defined by Klecka (1980) as that set of variables resulting from a stepwise variable selection method (in the present case, F-to-enter), whereby each variable provides a unique (non-redundant) contribution, relative to others in the subset, to discriminate among groups. Costanza & Afifi (1979) recommended a liberal alpha level for F-to-enter of $\alpha = 0.15$ to ensure entry of important variables into the CVA. This stepwise process minimized the potential for including highly intercorrelated variables in the CVA, as these may complicate the analysis (Klecka, 1980). Derived canonical variates were interpreted if they contributed to describing 90% of the cumulative proportion of total variation among groups. Tissot (1990) noted that when combined with biological interpretation, the 90% rule sufficiently separates real from trivial variates. Case scores were plotted in discriminant space with 95% confidence ellipses around each group centroid as an estimate of true population differences. The strength of association between groups and interpreted variates was determined with canonical correlation coefficients, R , which, when squared, indicate the proportion of variance shared between groups and variables on that canonical variate. Those variables most important in providing intergroup discrimination were identified with canonical loadings, r , correlations between the interpreted canonical variates

and variables (Tabachnick & Fidell, 1996). Standardized canonical coefficients revealed the size- or shape-related nature of interpreted variates (Pimentel, 1979).

A jackknifed group classification procedure was used on all specimens, where each specimen was classified using variates derived from the other 119 specimens, to test the classification success of the derived variates. Tabachnick & Fidell (1996) noted that the entry order of variables during a stepwise CVA may be biased by trivial relationships among variables within the sample that do not reflect true relationships in the population. To test the stability of the jackknifed classification procedure, and to test for variable entry bias, a split-sample validation procedure was used (Tabachnick & Fidell, 1996). In this procedure, canonical variates were recalculated using 96 (80%) randomly selected individuals (learning cases) from the original group of 120 specimens (12 per sex and habitat), and the remaining 24 individuals (test cases) were then classified to habitat using the newly derived variates (SYSTAT, 1996; Tabachnick & Fidell, 1996). Similarities in classification successes among the jackknifed, learning, and test runs were interpreted as evidence of model stability and minimal variable entry bias.

Inter- and Intra-habitat Sexual Dimorphism

The same statistical procedure described in the previous shell form section was used to determine: (1) if sexual dimorphism was evident within *A. carinata* using all individuals pooled; (2) those variables important in observed dimorphism, if present, and; (3) if dimorphism was consistent among all habitat groups.

Interhabitat Shell Patterning

All individuals were assigned to either "variegated" or "solid" color categories, based on the presence or absence of any deviation from a uniform, unpatterned exterior on the body whorl. Chi-square tests of constructed contingency tables were used to test the null hypothesis that color frequency was independent of group. Rejection of the null hypothesis (demonstrating non-independence) in the among-habitat test was followed with manipulations of the contingency tables to identify the disparate habitat(s) (Zar, 1996).

All statistics were calculated using version 6.0.1 of SYSTAT for Windows (SYSTAT, 1996). Dry shell vouchers of *Alia carinata* from each of the four habitats analyzed in this study are deposited at the Los Angeles County Museum of Natural History, Los Angeles, California, catalog numbers LACM 152413–152420.

RESULTS

Data Screening

Two univariate outliers were identified in the sex group screening process, and one case was identified as a mul-

tivariate outlier with both the habitat and sex group screening processes. The univariate outliers included a large female (8.4 mm ShHt) with an exceptionally large SpWd (2.7 mm, $z = 3.308$), and a large male (9.6 mm ShHt) with an exceptionally large ApHt (4.2 mm, $z = 3.421$). The multivariate outlier case was male ($D^2 = 26.917$) from MP ($D^2 = 28.546$) that displayed a very broad form (4.1 mm ShWd) relative to its unexceptional ShHt (7.5 mm). A log 10(\times) transformation of the variables SpWd and ApHt corrected the univariate outlier problems. The multivariate outlier case was deleted from the data set and replaced with a randomly selected individual from the same habitat and sex. A recheck of the new data set revealed no univariate or multivariate outliers, by either sex or habitat.

Interhabitat Shell Form

All variables, except ShWd, differed significantly among habitats (Table 2). Pairwise comparisons revealed that: *A. carinata* from ZM were generally short, with relatively small spires and apertures, and large apical and keel angles; specimens from GS were tall, with relatively large apertures; specimens from MP were tall, with relatively tall spires; and *A. carinata* from the RB habitat displayed features similar to those from MP.

The variable ShHt was significantly different among habitats ($F = 6.32$, $P < 0.001$, $df = 3$ and 116) and was designated as a covariate in ANCOVA. With the influence of size extracted or minimized, all variables tested were significantly different among habitats, demonstrating a substantial shape component in among-habitat variable differences (Table 3). The variables AA and KA were not analyzed because they did not relate significantly to the covariate. Pairwise comparisons showed that most variables tested also had substantial size components, as relationships among habitats differed from those detected with ANOVA. This analysis showed, independent of size, that: GS forms of *A. carinata* were narrow with small spires and large apertures; ZM forms were very broad with short spires; MP forms were fairly broad with tall spires; and RB forms displayed large spires and small apertures.

The ratio ShWd:ShHt, *sensu* Bergman et al. (1983), differed significantly among habitats (Table 2). Pairwise comparisons indicated that *A. carinata* from GS were significantly narrower than those from the RB and MP habitats. *Alia carinata* from ZM were significantly wider than all other habitat forms (Table 2). Shoulder keel development in *A. carinata*, *sensu* Bergman et al. (1983), was significantly different among the four habitats (Table 4). Pairwise comparisons of rank sums showed that keel development in specimens from GS was significantly less than that of the ZM ($q = 10.1$, $P < 0.001$, $df = 4$), MP ($q = 8.2$, $P < 0.01$), and RB ($q = 6.4$, $P < 0.01$) habitats. No other significant differences between paired rank sums

Table 2

ANOVA results for *Alia carinata* from four sampled habitats: subtidal rocky benthic (B), *Gastroclonium subarticulatum* (G), *Macrocystis pyrifera* (M), and *Zostera marina* (Z), $n = 30$ for each habitat. Means and standard errors for AA and KA in degrees, ShWd:ShHt unitless, all others in mm. Variable means significantly different (* $P < .05$, ** $P < .001$), not significantly different (ns), among habitats. P.C. = Bonferroni-adjusted t-test.

Variable	B		G		M		Z		ANOVA F (3,116)	P.C.
	Mean	SE	Mean	SE	Mean	SE	Mean	SE		
ShHt	7.36	0.09	7.74	0.16	7.59	0.09	7.11	0.08	6.32**	G, M > Z
ShWd	3.60	0.04	3.67	0.06	3.72	0.05	3.63	0.03	1.14 ns	
SpHt	2.62	0.04	2.60	0.06	2.68	0.05	2.34	0.04	10.00**	M, B, G > Z
SpWd	2.32	0.03	2.31	0.04	2.32	0.03	2.21	0.02	2.80*	B, M > Z
ApHt	3.03	0.03	3.31	0.07	3.14	0.03	3.03	0.03	8.41**	G > B, Z
ApWd	1.45	0.02	1.60	0.03	1.53	0.02	1.48	0.02	9.73**	G > Z, B
AA	41.6	0.3	41.8	0.4	41.0	0.4	43.5	0.2	11.54**	Z > G, B, M
KA	41.8	0.8	29.8	1.1	45.3	1.2	45.8	0.9	55.15**	Z > B > G; M > G
ShWd:ShHt	0.489	0.003	0.475	0.003	0.490	0.004	0.512	0.004	16.79**	Z > M, B > G

were detected. Only four percent (4%) of *A. carinata* from GS were strongly keeled (rating 3–5). In contrast, 97% of individuals from ZM, 87% from MP, and 80% from the RB habitat were strongly keeled.

Significant multivariate differences existed among habitat group forms ($F = 10.87$, $P < 0.001$, $df = 24$ and 316). The stepwise CVA revealed that the variables KA, SpWd, AA, ApWd, and ShHt (in decreasing order of relative importance) provided optimal information in discriminating among habitat forms; following entry of these five variables into the CVA, no other variables provided significant additional discrimination among groups. The first and second canonical variates (canonical correlations $r = 0.82$ and $r = 0.57$, respectively) together summarized almost 93% of the intergroup differences. The third canonical variate was not interpreted because it summarized less than 10% of the variation among groups. Most habitat group centroids were significantly different from each other using the five optimal variables on the first and second canonical variates, evidenced by non-overlapping 95% confidence ellipses around habitat centroids in Figure 2. However, no significant difference existed between

population forms of *A. carinata* from MP and RB habitats on the first or second variate.

Canonical loadings showed the relative importance of variables to each interpreted canonical variate (Table 5). Variate 1, summarizing 74.9% of intergroup variation, largely represented the variable KA (canonical loading $r = -0.81$), most important in separating GS forms of *A. carinata* from the other three habitat groups. Large positive scores on variate 1 represented relatively small shoulder keels. Less important were the variables ApWd ($r = 0.31$) and ShHt ($r = 0.19$). Large positive scores on variate 1 represented relatively large apertures widths and shell heights. The variables SpWd and AA did not contribute substantially to variation described on the first variate. The mix of positive and negative canonical coefficients on canonical variate 1 (Table 5) indicated that this variate primarily described shape, rather than size, differences among groups: GS forms of *A. carinata* were small-shouldered compared to RB, MP, and ZM habitat forms, independent of size.

The second variate, summarizing 17.8% of intergroup variation, largely represented the variable AA ($r = 0.69$),

Table 3

ANCOVA results for *Alia carinata* from four sampled habitats, $n = 30$ for each habitat. Adjusted (for covariate ShHt) means and standard errors in mm. All variable means significantly different (* $P < 0.001$) among habitats. P.C. = Bonferroni-adjusted t-test. KA, AA, and ShWd:ShHt not analyzed with ANCOVA, see text. Habitat abbreviations follow Table 2.

Variable	B		G		M		Z		ANCOVA F (3,115)	P.C.
	Mean	SE	Mean	SE	Mean	SE	Mean	SE		
ShWd	3.63	0.03	3.56	0.03	3.66	0.03	3.76	0.03	10.08*	Z > B, G; M > G
SpHt	2.65	0.02	2.49	0.02	2.62	0.02	2.47	0.02	19.54*	B, M > G, Z
SpWd	2.34	0.02	2.23	0.02	2.28	0.02	2.29	0.02	8.41*	B > M, G
ApHt	3.06	0.02	3.18	0.02	3.09	0.02	3.14	0.02	8.21*	G > M, B; Z > B
ApWd	1.46	0.02	1.56	0.02	1.51	0.02	1.52	0.02	7.21*	G, Z > B

Table 4

Number and percent of *A. carinata* by keel rating and habitat, $n = 30$ for each habitat. Extent of shoulder keel development evaluated using an assigned rating of 1 (least keeled) to 5 (most keeled). *G. subarticulatum* (G) rank sum significantly less ($H = 60.4$, $P < 0.001$, $df = 3$) than others at $\alpha = 0.05$. See Bergman et al. (1983) for illustrations of keel ratings. Habitat abbreviations follow Table 2.

Keel rating	Habitat			
	G	B	M	Z
1	11 (37%)	0	0	0
2	15 (50%)	6 (20%)	4 (13%)	1 (3%)
3	4 (13%)	12 (40%)	8 (27%)	6 (20%)
4	0	10 (33%)	13 (43%)	14 (47%)
5	0	2 (7%)	5 (17%)	9 (30%)
Rank sum	643.5	1862	2198.5	2556

most important in separating ZM forms of *A. carinata* from RB and MP forms (Figure 2). Large positive scores on variate 2 represented relatively large apical angles. Less important on canonical variate 2 were the variables KA ($r = 0.38$), SpWd ($r = -0.37$), and ShHt ($r = -0.32$). Large scores on variate 2 represented relatively large keel angles, and relatively small spire widths and shell heights. The variable ApWd did not load on variate 2 (Table 5). The mix of positive and negative coefficients on canonical variate 2 indicated that this variate also described shape differences among habitat forms. Specifically, specimens of *A. carinata* from ZM had larger apical angles, and by definition, greater whorl expansion rates, than specimens from either RB or MP habitats, independent of size. The CVA and the previous univariate analyses demonstrated that large apical angles in ZM forms of *A. carinata* were a consequence of shorter spire heights, rather than larger spire widths, relative to overall shell size.

Overall jackknifed classification success of habitat forms was moderately high (65.8%), with the following individual habitat forms of *A. carinata* correctly classified: RB 60%, GS 90%, MP 43.3%, and ZM 70% (Table 6). These percentages, with the exception of that for MP forms, are substantially higher than the 25% classification success that would statistically occur by chance alone. Classification results reflect canonical graph data (Figure 2), as *A. carinata* from the MP habitat were most often misclassified as RB forms.

In the split-sample validation procedure, stepwise CVA of 96 randomly selected specimens resulted in the identification of an optimal subset of variables that included KA, ApWd, AA, and SpWd, in descending order of relative importance. Variates derived from these variables and individuals resulted in the correct jackknifed classification of 62 of the 96 (64.6%) learning specimens. Six-

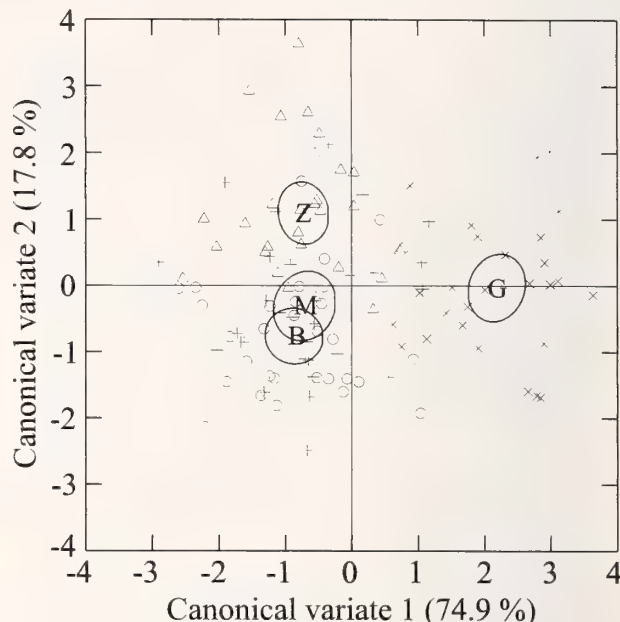


Figure 2

Plot of *Alia carinata* habitat groups on the first and second canonical variates. Letters (B, G, M, Z) represent locations of habitat group centroids, and symbols represent individual case scores (circles = benthic hard bottom, + = *Macrocystis pyrifera* canopy, x = *Gastroclonium subarticulatum*, triangles = *Zostera marina*, $n = 30$ for each habitat). Ellipses are 95% confidence limits for population group centroids. Relative percentages of total variation among groups explained by each variate are shown in parentheses.

teen of the 24 (67.7%) remaining test cases were then correctly classified using these derived variates. Individual habitat assignments in both the learning run and the test run closely resembled the habitat assignment percentages using all specimens (see Table 6). Consistency of results among all three classification runs indicated that the derived canonical variates summarized form variability among the sampled habitats well.

Table 5

Loadings and standardized coefficients by variable and canonical variate.

Variable	Variate 1		Variate 2	
	Loading	Coefficient	Loading	Coefficient
KA	-0.81	-0.90	0.38	0.29
ApWd	0.31	0.63	0.02	0.07
ShHt	0.19	0.64	-0.32	1.59
SpWd	0.04	-0.98	-0.37	-1.65
AA	-0.03	0.24	0.69	1.13

Table 6

Habitat assignment of *Alia carinata* using jackknifed canonical variate analysis. Habitat abbreviations follow Table 2.

Actual habitat	Predicted habitat				Total n
	B	G	M	Z	
B	18 (60%)	1 (3.3%)	7 (23.3%)	4 (13.3%)	30
G	1 (3.3%)	27 (90%)	1 (3.3%)	1 (3.3%)	30
M	7 (23.3%)	3 (10%)	13 (43.3%)	7 (23.3%)	30
Z	5 (16.7%)	0	4 (13.3%)	21 (70%)	30
Total	31	31	25	33	79 (65.8%)

Inter- and Intra-habitat Sexual Dimorphism

All variables except AA were significantly larger in males (Table 7). After removing or reducing the effects of size using ANCOVA, no significant differences existed between sexes for every variable tested (Table 8), indicating that sexual dimorphism was a result of size differences. The variable ShWd was not analyzed with ANCOVA because it did not meet the assumption of between-group homogeneity of slopes, and the variable KA was not analyzed because it did not display a significant linear relationship with the covariate.

Significant differences existed between sex forms with all habitats pooled ($F = 2.66$, $P = 0.01$, $df = 8$ and 111). Stepwise CVA showed that the variable ShWd alone provided optimal information in discriminating among sexes. That is, after its entry into the CVA, no other variables contributed significant additional discrimination between sexes. This result indicated that the variables used in this sex analysis were highly intercorrelated and contained the same discriminating information. Although sex group centroids (based only on ShWd) were significantly different, jackknifed classification success was relatively

low, with males and females correctly classified 63% and 72% of the time, respectively.

Within-habitat analysis helped to explain the low canonical correlation coefficient ($R = 0.35$) for this pooled analysis. No multivariate form differences were detected between sexes within the habitats MP ($F = 0.69$, $P = 0.70$, $df = 8$ and 21) or ZM ($F = 0.55$, $P = 0.81$), while significant form differences did exist within the RB ($F = 2.43$, $P = 0.049$) and GS habitats ($F = 12.22$, $P < 0.001$). The variable ShWd provided optimal information in separating RB habitat population sex centroids, and the derived variate ($R = 0.60$) correctly classified males and females 80% and 73% of the time, respectively. The variable SpWd provided optimal information to separate GS forms of *A. carinata* population sex centroids, and the derived variate ($R = 0.71$) correctly classified males and females 80% and 93% of the time, respectively. In summary, CVA showed that multivariate models were no more useful than univariate analysis of standardized scores (z -scores) in discriminating between sexes. The sex ratio of *A. carinata* approximated unity ($\chi^2 = 0.25$, $P = 0.62$, $df = 1$) and did not differ among the four habitats ($\chi^2 = 0.57$, $P = 0.90$, $df = 3$).

Table 7

ANOVA results for *Alia carinata* by sex, $n = 60$ for each sex. Means and standard errors for AA and KA in degrees, all others in mm. Variable means significantly different (* $P < 0.05$, ** $P < 0.001$), not significantly different (ns), between sexes.

Variable	Males		Females		ANOVA F (1,118)
	Mean	SE	Mean	SE	
ShHt	7.66	0.09	7.25	0.06	13.43**
ShWd	3.74	0.03	3.56	0.03	16.14**
SpHt	2.65	0.04	2.46	0.03	14.13**
SpWd	2.34	0.02	2.24	0.02	12.15**
ApHt	3.19	0.04	3.07	0.03	6.49*
ApWd	1.55	0.02	1.48	0.01	8.08*
AA	41.6	0.3	42.3	0.2	0.65 ns
KA	41.3	1.1	40.1	1.1	4.25*

Table 8

ANCOVA results for *Alia carinata* by sex, $n = 60$ for each sex. Adjusted (for covariate ShHt) means and standard errors for AA in degrees, all others in mm. Variable means not significantly different (ns) between sexes.

ShWd and KA not analyzed with ANCOVA, see text.

Variable	Males		Females		ANCOVA F (1,117)
	Mean	SE	Mean	SE	
SpHt	2.57	0.02	2.54	0.02	1.24 ns
SpWd	2.29	0.01	2.28	0.01	0.50 ns
ApHt	3.11	0.02	3.13	0.02	1.72 ns
ApWd	1.52	0.01	1.51	0.01	0.20 ns
AA	41.9	0.2	42.0	0.2	0.17 ns

Interhabitat Shell Patterning

The distribution of solid and variegated *A. carinata* individuals within habitats was significantly different among habitat groups ($\chi^2 = 12.80$, $P < 0.01$, $df = 3$). Sixty-eight percent of *A. carinata* from ZM were solid and dark brown to almost black. In contrast, 60–77% of individuals were variegated in other habitats. Solid specimens from non-ZM habitats tended to be lighter in color, ranging from light to dark brown, to bright orange. No significant difference was detected in the pattern frequencies among the RB, GS, and MP groups ($\chi^2 = 1.93$, $P = 0.38$, $df = 2$). Observed variegations included dark brown to whitish triangular polygons, irregular dots, spiral lines, and spiral and axial tessellations distributed over all or portions of the shell. Many of the specimens from the MP habitat were characterized by a light-colored band on the shoulder carina, as were several of the RB specimens. This pattern was not observed in *A. carinata* from either GS or ZM habitats. Variegations were more pronounced in *A. carinata* from GS compared to other habitats. There was no relationship between pattern presence and sex ($\chi^2 = 1.69$, $P = 0.19$, $df = 1$).

DISCUSSION

Alia carinata shell forms were distinct and quantitatively separable in three of four sampled habitats, and observed color variants generally corroborated the observations of Carter & Behrens (1980). Specimens from GS were generally tall and narrow, and often lacked the characteristic shoulder carina that has been used as a key taxonomic feature of this species (Carlton & Roth, 1975; McLean, 1978; Abbott & Haderlie, 1980). In addition, GS forms possessed large apertures and were generally light in color with pronounced shell pattern variegations. The ZM forms were short, broad, and stout, and were characterized primarily by relatively large apical angles. More often than not, they were dark and unpatterned, and displayed very large shoulder carinas (keel angles). The RB forms were less distinct than the previous two habitat forms, but were characterized by moderate shoulder carina development and small apertures. The RB and MP forms of *A. carinata* were statistically indistinct, though the latter often possessed characteristic, light-colored shoulder carinas and narrow spires. These results also corroborate those of Bergman et al. (1983), where ShWd:ShHt ratios of 0.526 and 0.469 from protected and exposed habitats, respectively, were reported in *A. carinata* from the Bodega Bay, California region. Comparable ratios and habitats from the present study are 0.512 and 0.475 from ZM (protected) and GS (exposed), respectively. Bergman et al. (1983) also reported that 9% and 81% of *A. carinata* from exposed and protected environments, respectively, were strongly keeled (rating 3–5), comparing favorably with the keel rating results from GS (4%) and ZM (97%) habitats in the present study.

In general, shell forms documented in this study agree well with causal relationships summarized by other research. Wave exposure is correlated with the presence of large apertures (Vermeij, 1978; Rugh, 1977) and narrow shell forms (Bergman et al., 1983; Trussell, 1997b), consistent with features of specimens from intertidal GS. Narrow forms may allow individuals to seek refuge in crevices during extreme wave exposure—crevices that may be unavailable to sharply keeled or broad-formed individuals (Trussell, 1997b). The RB and MP specimens of *A. carinata* from deeper and presumably cooler water had taller spires and smaller AA's than those from most other habitats, which may indicate slower growth rates and consequent reduced whorl expansion rates (Frank, 1975; Phillips, 1981; Hughes, 1986). Small apertures in RB specimens, and stout shells and short spires in ZM forms of *A. carinata* may protect against the aperture peeling and spire crushing techniques often used by crabs when preying on gastropods (Vermeij, 1978).

Crabs are known to exert considerable predation pressure on small gastropods (Vermeij, 1977, 1978; Trussell, 1996), with pressure generally highest in protected, lower energy areas (Trussell, 1996). Bergman et al. (1983) hypothesized that large shoulder keels and broad shells in *A. carinata* from wave-protected habitats (i.e., harbor) were adaptive responses to crab predation pressure. They substantiated this conclusion by noting that shell scars, indicative of failed crab predation attempts (Vermeij, 1978), were more frequent in the protected habitat relative to an exposed habitat. While I did not collect quantitative data on sympatric durophagous crab species—specifically rock crabs, *Cancer* spp., and hermit crabs, Paguridae (Spight, 1976; Vermeij, 1977; Gosselin & Chia, 1995)—abundance by habitat, there did appear to be relatively higher numbers of both crab groups in the RB and ZM habitats, and a noticeably greater number of scarred *A. carinata* in the RB habitat. In one recent study, however, snails only needed to be proximal to, not attacked by, crab predators to elicit adaptive morphologic responses (Trussell, 1996, in *Littorina* sp.). He speculated that chemical or visual cues by prey, or chemical cues by predatory crabs, may have engendered this response. Globose forms of *A. carinata* from ZM may indicate an adaptive response to the relatively large numbers of *Cancer* spp. in this habitat. Bergman et al. (1983) presented preliminary observations which indicated that small *Cancer* sp. were more successful at damaging and killing unkeeled, versus keeled, *A. carinata*. While breaking *A. carinata* shells for sex determinations in this study, I noted that specimens from ZM were much more difficult to crush than those from other sampled habitats. A study of shell compression strengths and crab presence/absence, by habitat, would be a quantitative test of this observation, although Vermeij (1978) noted that studies of this nature often produce highly variable results.

Less easily explained using known causal relationships

is the large shell size in forms of *A. carinata* from GS. Trussell (1997a) showed that larger individuals (e.g., *Littorina* sp.) were often selected against by wave dislodgement, while Brown & Quinn (1988) speculated that foraging efficiency may be reduced in larger individuals (e.g., *Collisella* spp. and *Nucella* sp.) trying to maintain their position in the high-energy intertidal zone, resulting in smaller overall sizes. I cannot explain the mechanisms directly responsible for the large shell size of open-coast forms of *A. carinata* from GS, but speculate that their large foot area, inferred from their large aperture area (Grahame & Mill, 1986; Trussell, 1997b), may increase substrate attachment in a comparatively food-rich environment (Leigh et al., 1987).

It is interesting that the CVA was unable to separate MP from RB forms of *A. carinata*. Although RB specimens displayed unique characteristics relative to other habitats, a large degree of overlap with MP forms confounded the separation. My recent field observations indicate that RB habitat *A. carinata* sub-adults and adults may migrate from this habitat to the MP canopy to deposit egg masses, rather than settling on the latter as juveniles. This suspected migration appears to coincide with the spring regeneration and growth of MP following annual kelp removal by winter storms. The present morphometric analysis suggests that RB habitat forms of *A. carinata* remain unchanged significantly during their tenure on MP.

Observed interhabitat sexual dimorphism disparities are also interesting. Purchon (1977) noted that sexual dimorphism in mollusks is rare. However, when present, it is usually size- and not shape-related (Webber, 1977), and is more common in the higher orders of the Gastropoda (Dobberteen & Ellmore, 1986). In cases where dimorphism is present, and unlike *A. carinata*, females are generally larger or more globose than males to facilitate the storage or brooding of eggs (e.g., Lindberg, 1985, *Margarites* sp. (Trochidae); Armengol, 1996, *Potamolithus* spp. (Hydrobiidae). I cannot explain the among-habitat differences in the presence or absence of conchological sexual dimorphism in sampled *A. carinata*. Sample sizes may have been inadequate to detect subtle differences in size between sexes in *A. carinata* from MP and ZM habitats: males from MP were taller than females (7.69 mm and 7.50 mm ShHt, respectively), though not significantly so, while males and females from ZM were similarly tall between sexes (7.06 mm and 7.15 mm ShHt, respectively). Having already speculated that MP specimens of *A. carinata* may have been RB migrants, I would expect similar sexual dimorphism in individuals from both of these habitats.

Shell color and pattern variability in gastropods are often linked to predation-related crypsis (Vermeij, 1978; Dytham et al., 1990, *Littorina* spp.; Cook & Bridle, 1995, *Littoraria* sp. Littorinidae; Gardner et al., 1995, *Clithon* sp. Neritidae;). Analysis of shell patterning in *A. carinata*

within and among habitats does not indicate a clear relationship with crypsis contributing to shell form variability. Variegated patterning and light base coloration did allow GS specimens of *A. carinata* to blend well with variably colored algal thalli and entrapped shell fragments. However, if predation-induced crypsis was important, I would expect that individuals from MP, the only homogeneously colored habitat, would be non-variegated and light to dark brown; however, they were not. The distinctive, variegated color form of *A. carinata* from MP, consisting of a whitish band on the body whorl carina, is quite obvious when observed and is the model color form for the mimic amphipod *Pleustes platypa* (Crane, 1969). This color form appears to be largely specific to MP, as it was not evident in specimens from GS or ZM habitats. My infrequent observations of this color form on RB habitats were more often than not near *Macrocystis* beds, and these likely represented individuals displaced from the MP canopies. *Alia carinata* from ZM were also very conspicuous in their habitat, being solid and dark on a light and variegated background. I have no direct explanation for this apparent lack of crypsis, as durophagous crabs were relatively abundant on the benthic substrate near the ZM habitat. Cook & Bridle (1995) speculated that the lack of crypsis in variably colored *Littoraria* sp. from canopies of mangroves and the presence of crypsis in the same species found on the trunk potentially resulted from a lack of crab predators and consequent lack of selection pressure in the former habitat. This may be true for *A. carinata* as well, as I have never observed *Cancer* spp. or large (> 1 cm) pagurids in either MP or ZM canopies.

Shell form variability in mollusks can be genetically based (Crothers, 1984; Grahame & Mill, 1993; Gosselin & Chia, 1995; Wilbur & Gaffney, 1997), a consequence of natural selection and adaptation. Variability can also be due to phenotypic plasticity as a response to the physical and biological environment (Palmer, 1990; Grahame et al., 1990; Chapman, 1994, 1995; Trussell, 1996). In those variable species that demonstrate direct development life-histories, both mechanisms may be important. However, in those taxa that disperse by settlement of planktonic larvae or juveniles, as do *Alia carinata*, genetic polymorphism is less likely. Rather, form variability should result from phenotypic plasticity or post-settlement selection. Bergman et al. (1983) suggested that between-exposure form variability in *A. carinata* may have represented a polymorphism due to the limited ability of "crawl away larvae" to disperse among habitats. Recent literature indicating that *A. carinata* demonstrate planktotrophic life histories (McLean, 1996) would suggest ecophenotypic adaptation, rather than genetic polymorphism. My qualitative and successive observations of form variability following recruitment events, and the lack of discontinuous shell phenotypes (Ford, 1940) also argue against polymorphism. Post-settlement selection, however, remains a likely mechanism in observed inter-

habitat shell form differences—in particular, selection for hydrodynamic, narrow forms in the wave-swept intertidal (Trussel, 1997b), and selection for stout, highly keeled forms in areas populated with durophagous crab species (Trussel, 1996). Although this study strongly suggests the existence of habitat-specific forms in *A. carinata*, a sampling design that included replication within habitats among regions, through at least a complete year, would be necessary to account for microhabitat (Chapman, 1995), geographic (Chow, 1987), and temporal (Gardner et al., 1995) influences on shell form. This last factor may be particularly important when considering potential among-year variation in growth rates and shell morphology due to periodic oceanographic events (e.g., El Niño/ENSO), not uncommon in California.

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Remains of the Prey—Recognizing the Midden Piles of *Octopus dofleini* (Wülker)

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Abstract. We described the contents and the field signs of 52 midden piles found outside occupied dens of *Octopus dofleini* (Wülker, 1910) in Prince William Sound and Cook Inlet, Alaska. The contents of midden piles are important data for describing octopus diets; yet the field signs for distinguishing octopus midden piles from remains left by other processes can be subtle. Remains of four crab species, *Telmessus cheiragonus* (Telesius, 1815), *Cancer oregonensis* (Dana, 1852), *Pugettia gracilis* Dana, 1851, and *Lophopanopeus bellus* (Stimpson, 1860), composed 74% of the prey individuals represented in intertidal middens in Prince William Sound. However, the same species were not typical of other locations: *Chlamys hastata* (Sowerby, 1843) and *C. rubida* (Hinds, 1845) were the most common species represented in subtidal middens, while the crab *P. gracilis* Dana, 1851, and the mussel *Mytilus trossulus* Gould, 1850, were among the most common in intertidal middens found in Cook Inlet. Drills were found on the hard remains of six species of crabs (75% of eight Crustacea species, 27% of 22 total species). Fifty-six percent of drill marks on crab species were located toward the carapace posterior. Of the crab species sampled in Prince William Sound that were drilled at all, *C. oregonensis* was the species most often drilled (36%), whereas *T. cheiragonus* was drilled least often (6%). Drills of *O. dofleini* on crabs were oblong ($2-6 \times 1-2.5$ mm), and came to a point at one or both ends. Drill marks tapered toward the inside of the shell, and when the final perforation of the inner surface was made, the drill was no more than a pinpoint. A previously undescribed mark in prey remains, the bite mark, occurred on the leg of *T. cheiragonus*. Bites on weathered prey remains were about 1.2 cm long \times 0.5 cm wide, occurring on the inside and outside of the leg.

INTRODUCTION

Animal “signs,” including tracks, scat, wallows, nests or dens, and bones, feathers, or other remains of prey, have been important data in studies of many different species, and have been used to indicate presence or absence, to estimate population size, breeding activity, and foraging ranges, and to examine diet. A great many marine organisms also leave “sign,” particularly the remains of hard-shelled prey. For example, in the northeastern Pacific, sea otters feed on clams and discard the shells (Kvitek et al., 1992). *Pycnopodia helianthoides* (Brandt, 1835), the sunflower star, also hunts clams, sometimes in the holes dug by sea otters. Sea stars push the sediment out of the way leaving behind a berm of sand or gravel and the empty shells of their bivalve prey (Kvitek et al., 1992). Octopuses feed on many different bivalves and clams, including *Saxidomus giganteus* Deshayes, 1839, which is also a prey of otters (Riedman & Estes, 1988), and discard the remains in midden piles (Hartwick et al., 1981; Hartwick & Thorarinsson, 1978; Mather, 1991, 1994; Mather & O’Dor, 1991). Distinguishing whether a clam has been opened by a sea otter, a sea star, or an octopus is useful for determining impacts of predators on invertebrate communities, requires specialized knowledge, and can limit research in some studies (e.g., Fotheringham, 1974; Kvitek et al., 1992).

Determining how animal remains arrived at their present location on a beach or on the sea floor requires paying attention to sometimes subtle clues (e.g., Fotheringham, 1974). Even so, identifying the source of animal remains can be an important research tool. Descriptions of prey middens have been a primary method of describing octopus diets; for example, in a sample of 12 papers investigating the diet of octopuses (Table 1) midden analysis was used in eight. Octopuses are often mobile and leave midden piles behind, so that the absence of an octopus at a midden pile does not necessarily imply that the remains were left by some other predator. Despite this, few descriptions of the “signs” left by octopuses have been published (but see Hartwick et al., 1978; Ambrose, 1983) to assist the beginning octopus researcher or to be used by someone working on species other than octopuses, but interested in attributing marine invertebrate remains to the animals that killed them. In this paper, we report field signs indicative of the presence of *Octopus dofleini* on beaches in Prince William Sound and Cook Inlet, Alaska, and describe the methods by which middens left by *O. dofleini* may be recognized.

From captive studies, octopuses, including *O. dofleini*, are known to use three different techniques to gain entry to hard-shelled prey: they may pull it apart, “drill” through the shell (Nixon, 1979; Hartwick, 1981), or bite it open (Anderson, 1994). The latter two methods leave

Table 1
Methods used to determine diet in a sample of octopus studies.

Species studied	Method of determining diet	Location	Source
<i>Octopus dofleini</i>	stomach contents	Japan, review article	Mottet, 1975
<i>O. dofleini</i>	midden counts	British Columbia	Hartwick et al., 1981
<i>O. dofleini</i>	midden counts	British Columbia	Mather et al., 1985
<i>O. dofleini</i>	midden counts	British Columbia	Cosgrove, 1987
<i>O. dofleini</i>	observation	Washington, captive study	Anderson, 1991
<i>O. dofleini</i>	midden counts	Washington	Anderson, 1994
<i>O. dofleini</i>	midden counts	Alaska	Vincent et al., 1998
<i>O. rubescens</i>	midden counts	California	Laidig et al., 1995
<i>O. vulgaris</i>	midden counts	South Africa	Smale & Buchan, 1981
<i>O. vulgaris</i>	midden counts	Bermuda	Mather & O'Dor, 1991
<i>O. vulgaris</i>	midden counts	Bermuda	Mather, 1991
<i>O. vulgaris</i>	stomach contents	Spanish Mediterranean	Sanchez & Obarti, 1993

marks on the prey that may be used to identify remains left by octopuses. The drill mark has frequently been mentioned in the literature (e.g., for *O. dofleini*, Hartwick et al., 1978, 1981; Hartwick, 1983), but described for *O. dofleini* only on *Saxidomus giganteus*, a bivalve (Ambrose et al., 1988). In this paper, we provide the first published descriptions of *O. dofleini* drills on crab species.

METHODS

Three study sites, Port Graham in Cook Inlet (59°21'N, 151°49'W) and Green (60°14'N, 147°14'W) and Montague (60°16'N, 147°26'W) Islands in Prince William Sound were surveyed for *Octopus dofleini*. The surveys consisted of intertidal beach walks and SCUBA dives, to depths of 33 m below mean lower low water (MLLW). Dens were identified by the presence of an octopus. If den litter was present at an occupied den, all bits were collected for later measurement and identification (following Foster 1991 for bivalves and Kozloff 1987 for all other taxa). Remains were judged to be either fresh (without algae growth on inner surfaces and unweathered) or old (either with algal growth or weathered). Old remains were not counted and measured as part of the octopus midden, as these remains may have been buried in the sediment until excavated by the octopus when making its den. All specimens collected were inspected for octopus drills or other signs of handling by octopus, and the locations of such marks were noted. Measurements of the lengths and widths were taken of bivalves, crab carapaces, and crab legs.

RESULTS

Prey remains were collected from 52 intertidal and subtidal sites located outside occupied dens and attributed to *Octopus dofleini* on the basis of the octopus in attendance. Middens characteristically contained crab remains: for

example, of the 42 middens found at intertidal dens in Prince William Sound, 40 contained at least one item from a crab. The most common species in these intertidal middens were *Telmessus cheiragonus*, *Cancer oregonensis*, *Pugettia gracilis*, and *Lophopanopeus bellus*, which together composed 74% of the sample of prey (estimated minimum individuals represented by midden items, Table 2). However, middens in other locations often had a different composition. Subtidal middens, collected from the same areas in the Sound but from depths between -5 and -33 m MLLW, were dominated by remains of scallops and other bivalves, rather than of crabs (Table 3); while four intertidal middens from Port Graham (in Cook Inlet, Alaska) contained a mixture of crabs and bivalves, but the most abundant species there were not the same as in the Sound (Table 4).

Inspection of midden remains sometimes revealed marks left by the octopus: we found both "drill" and "bite" marks (Figure 1). The drill mark of *O. dofleini* on carapaces of *Cancer oregonensis* and *Lophopanopeus bellus* (Figure 1a) was oblong, about 1.5–3.0 millimeters long and 0.25–2.0 millimeters wide, and usually came to a point at one or both ends. The drill gradually tapered from the outside of the shell toward the inside. The final perforation of the inner surface may be no more than a pinpoint. The only other drill marks that we found on shells in this area (not in octopus middens) were moon snail drill marks that were larger and almost perfectly round, and were readily distinguishable by size and shape from the marks of *Octopus dofleini*. Drills were found on the carapace or chelipeds of six species of prey (27% of 22 species found in middens, Tables 2–5).

Drill marks were more frequently encountered on some species than others. Of the crab remains found in intertidal middens in the Sound (Table 2), the carapaces of *Cancer oregonensis* and of *Pugettia gracilis* were most often drilled, while those of *Telmessus cheiragonus* were

Table 2

Prey remains found in 42 intertidal midden piles left by *Octopus dofleini* on Green and Montague Islands, Prince William Sound, AK.

Taxon	Species	Count found ¹ (prop. of sample in parentheses)	No. drilled	Avg. size ² (sample size)
Decapoda	<i>Telmessus cheiragonus</i> (Telesius, 1815)	70 (0.30)	4 (0.06)	3.55 (70)
Decapoda	<i>Cancer oregonensis</i> (Dana, 1852)	58 (0.25)	21 (0.36)	1.99 (55)
Decapoda	<i>Pugettia gracilis</i> Dana, 1851	23 (0.10)	6 (0.26)	2.77 (21)
Decapoda	<i>Lophopanopeus bellus</i> (Stimpson, 1860)	20 (0.09)	2 (0.10)	1.57 (18)
Bivalvia	<i>Macoma inquinata</i> (Deshayes, 1855)	17 (0.07)	0	2.75 (15)
Bivalvia	<i>Protothaca staminea</i> (Conrad, 1837)	17 (0.07)	0	2.16 (16)
Bivalvia	<i>Saxidomus giganteus</i> Deshayes, 1839	8 (0.03)	0	2.63 (8)
Gastropoda	<i>Littorina sitkana</i> Philippi, 1845	4 (0.02)	0	
Bivalvia	<i>Chlamys hastata</i> (Sowerby, 1843)	3 (0.013)	0	3.83 (3)
Bivalvia	<i>Pododesmus macroschisma</i> (Deshayes, 1839)	3 (0.01)	0	6.40 (3)
Polyplocophora	<i>Tonicella lineata</i> (Wood, 1815)	2 (0.01)	0	1.20 (1)
Bivalvia	<i>Mytilus trossulus</i> Gould, 1850	2 (0.01)	0	1.95 (2)
Decapoda	<i>Cancer productus</i> Randall, 1839	2 (0.01)	0	6.00 (1)
Decapoda	<i>Cryptolithodes sitchensis</i> Brandt, 1853	2 (0.01)	0	
Bivalvia	<i>Chlamys rubida</i> (Hinds, 1845)	1 (0.004)	0	
Decapoda	<i>Hapalogaster mertensii</i> Brandt, 1850	1 (0.004)	0	
Decapoda	<i>Phyllolithodes papillosus</i> Brandt, 1849	1 (0.004)	0	5.0 (1)
Gastropoda	<i>Trichotropis cancellata</i> Hinds, 1849	1 (0.004)	0	10.5 (1)

¹ For crabs, only the number of carapaces is given, indicating the minimum number of individuals represented in the litter; for bivalves, each count indicates either the left valve, right valve, or both when still attached.

² The mean of the carapace length (cm) for crabs and of valve length for bivalves. Sample size is indicated in parentheses (in some cases, remains were broken and could not be measured, although the fragments could be identified to species).

only infrequently drilled. In contrast to crabs, most bivalves were not drilled (Tables 2–4). *Chlamys* sp. valves found at both intertidal and subtidal dens were never drilled ($n = 19$), nor were any other bivalves collected in the Sound (Tables 2 & 3). However, drills were recorded on four bivalves from middens in front of unoccupied dens in Port Graham (Figure 1b).

We also examined the locations of drill marks on crab remains, using a sample of 50 drilled carapaces and 21 drilled chelipeds (of all species) collected from midden piles at both occupied and unoccupied dens in Prince William Sound (including remains in Tables 2, 3, 5, and ad-

ditional remains not listed). Each item was drilled only once. On carapaces, 38% of the drills ($n = 19$ of 50) were placed over the posterior midline (Figure 2a). Additional drills were placed immediately to the right ($n = 6$) or to the left ($n = 3$) of the posterior midline, so that 56% ($n = 28$) of the drills were located in the posterior medial portion of the carapaces. The next most common position drilled was over the medial central portion of carapaces ($n = 18$ or 36%), including drills on the central midline ($n = 9$) and immediately to the right ($n = 4$) or left ($n = 5$) of midline. The remaining 8% of the drills ($n = 4$) were located in the left posterior section of the

Table 3

Prey remains found in six subtidal midden piles left by *Octopus dofleini* near Green and Montague Islands, Prince William Sound, AK.

Taxon	Species	No. found ¹	No. drilled	Avg. size ¹
Bivalvia	<i>Chlamys hastata</i> (Sowerby, 1843)	9 (0.24)	0	2.46 (9)
Bivalvia	<i>Chlamys rubida</i> (Hinds, 1845)	6 (0.16)	0	2.23 (6)
Bivalvia	<i>Macoma inquinata</i> (Deshayes, 1855)	5 (0.14)	0	3.58 (5)
Decapoda	<i>Cancer oregonensis</i> (Dana, 1852)	5 (0.14)	4 (0.80)	1.68 (5)
Decapoda	<i>Pugettia gracilis</i> Dana, 1851	4 (0.11)	0	2.70 (3)
Decapoda	<i>Lophopanopeus bellus</i> (Stimpson, 1860)	4 (0.11)	0	1.68 (4)
Gastropoda	<i>Acmaea</i> sp.	3 (0.08)	0	1.73 (3)
Bivalvia	<i>Pododesmus macroschisma</i> (Deshayes, 1839)	1 (0.03)	0	2.60 (1)

¹ Details as in Table 2.

Table 4

Prey remains found in four intertidal midden piles left by *Octopus dofleini* Port Graham, Cook Inlet, AK.

Taxon	Species	No. found ¹	No. drilled	Avg. size ¹
Decapoda	<i>Pugettia gracilis</i> Dana, 1851	7 (0.35)	0	2.63 (7)
Bivalvia	<i>Mytilus trossulus</i> Gould, 1850	4 (0.20)	0	2.98 (4)
Decapoda	<i>Cancer oregonensis</i> (Dana, 1852)	3 (0.15)	2 (0.67)	2.17 (3)
Bivalvia	<i>Protothaca staminea</i> (Conrad, 1857)	2 (0.10)	0	1.95 (2)
Bivalvia	<i>Macoma nasuta</i> (Conrad, 1837)	1 (0.05)	0	1.80 (1)
Gastropoda	<i>Nucella emarginata</i> (Deshayes, 1839)	1 (0.05)	0	2.70 (1)
Gastropoda	<i>Nucella lima</i> (Gmelin, 1791)	1 (0.05)	0	2.60 (1)
Bivalvia	<i>Saxidomus giganteus</i> Deshayes, 1839	1 (0.05)	0	2.60 (1)

¹ Details as in Table 2.

carapaces. Chelipeds were drilled on both inner (67%) and outer surfaces (33%) (Figure 2b, c), most commonly over the cheliped midline, but occasionally dorsal or ventral of the midline. We observed only one drill that was beyond the cheliped joint, but still on the leg of the crab. The Port Graham bivalves ($n = 4$) were drilled toward the posterior of the umbo (Figure 1b).

A previously undescribed mark, which we term the "bite mark" (Figure 1c), was found exclusively on the penultimate segment of the 1st (cheliped) leg of *Telmessus cheiragonus*. As implied by the name, we believe the bite mark is made when the octopus uses its beak to bite through the leg of this prey species. Bite marks were oval in shape and greatly varied in size depending on the amount of weathering of the remains. In the freshest specimens, bite marks were about 1.2 cm long \times 0.5 cm wide, located on the inside of the leg, and extending the entire length of the segment. The bite mark is apparently placed at a weak point in the leg exoskeleton and has a tendency to expand as prey remains break down. Bite marks were not found on the legs of other prey species; however, only five legs from species other than *T. cheiragonus* were examined. Of the 1st legs examined ($n = 112$) from Prince William Sound 29% (32) had bite marks. No bite marks were recorded from Port Graham, although only four *T. cheiragonus* 1st legs were found in that area.

DISCUSSION

We describe remains found in 52 middens found outside the dens of *Octopus dofleini* in order to assist beginning octopus researchers (or those expert on species other than octopuses) in recognizing an octopus midden. The composition of the midden may be helpful, as most middens consisted primarily of crab and bivalve remains. Most middens in the intertidal in Prince William Sound contained one or more of four crab species (Table 2), so that this species composition was characteristic of middens. However, the characteristic species were different at different depths and geographic locations (compare with Tables 3, 4). The local distinctiveness of octopus midden piles has been noted in several papers detailing that oc-

topuses in different areas eat different species or handle prey differently (References in Table 1), but may also result from factors influencing the residence time of prey remains in middens under different conditions (Ambrose, 1983; Mather, 1991). Closer inspection of prey remains from middens revealed that octopuses left marks on some of their prey during the process of killing and consuming them. However, some species of prey were more likely to be marked than others, and most items in middens were not marked by the octopus. In our sample, three species of crabs were likely to be drilled on the carapace (Tables 2–4) or a cheliped (Table 5), and a "bite" mark was often found on the leg of the crab *Telmessus cheiragonus*. However, most items of any species, and almost all bivalve remains examined, bore no mark of being handled by *O. dofleini*.

Octopuses typically drill many of their hard-shelled prey. The behavior has been reported for a number of octopus species (*Octopus dofleini*: Hartwick et al., 1978; Ambrose et al., 1988; *O. bimaculatus* Verrill and *O. bimaculoides* Pickford & McConnaughey: Pilson & Taylor 1961; *O. mimus* Gould, 1852: Cortez et al., 1998; *Eledone cirrhosa* (Lamarck): Boyle & Knobloch, 1981; Grisely et al., 1996) and studied in detail in *O. vulgaris* Cuvier, 1797 (discussed in Nixon & Maconnachie, 1988). The average dimensions of holes drilled by *O. dofleini* in the butter clam were 1.03 mm on the outer surface of the shell and 0.56 mm on the inner surface of the shell (Ambrose et al., 1988), while drill holes made by *O. vulgaris* on *Mytilus* sp. were round with average dimensions of 1.1 mm on the outer surface and only 0.2 mm on the inner surface. In the latter species, drill holes were made primarily with the salivary papilla (Nixon, 1980), the secretions of which dissolve the shell (Nixon & Maconnachie, 1988). Multiple drill holes were common on an individual prey item of *O. vulgaris* (Nixon, 1979). On bivalves, *O. vulgaris* usually placed holes over the adductor muscle (Nixon & Maconnachie, 1988); and salivary toxins were secreted through the hole to paralyze, kill, or partially digest the prey.

Some octopuses drill crustaceans as well as bivalves

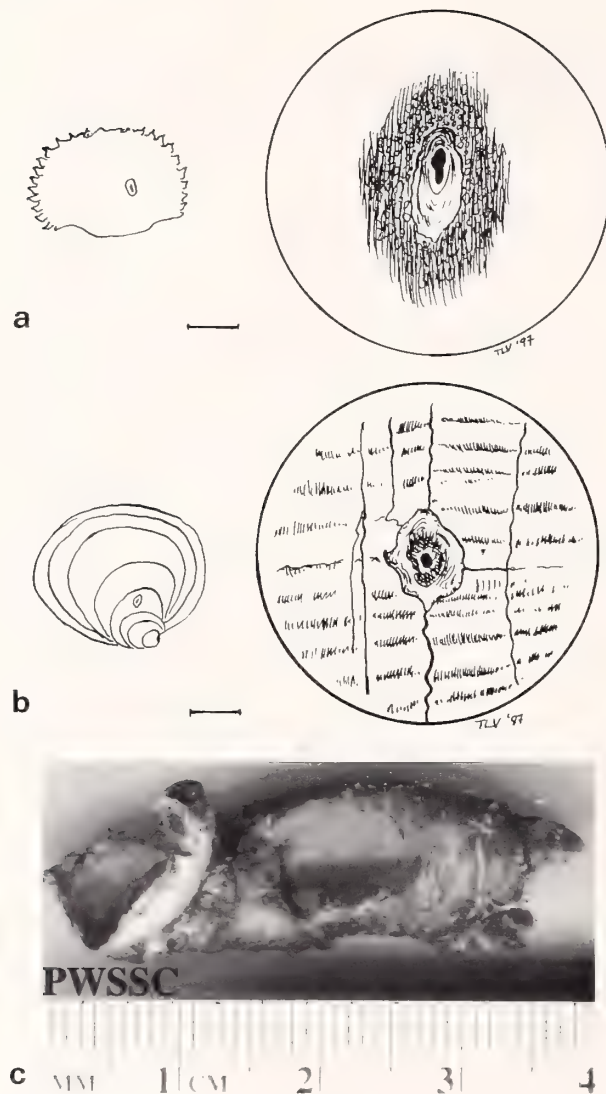


Figure 1

Illustrations of the marks found in the prey remains of *Octopus dofleini*: typical drill mark on (a) the carapace of the Oregon Cancer crab, *Cancer oregonensis*, and (b) the umbo of the bivalve, *Protothaca staminea* (the circle shows the view through a microscope; the scale bar shows one millimeter); and (c) typical bite mark on the leg of the helmet crab, *Telmessus cheiragonus*. At the time of publication, images of these and other prey remains from octopus middens are available at www.pwssc.gen.ak.us/~dls/octopus/specimens/ on the world-wide web.

(*Octopus vulgaris*, Guerra & Nixon, 1987; *Eledone cirrhosa*, Boyle & Knobloch, 1981; Grisley et al., 1996). Although drilling as a predatory behavior against mollusks has been described in detail (e.g., Pilson & Taylor, 1961; Nixon, 1979; Ambrose et al., 1988; Nixon & Macconnachie, 1988), work with crustaceans has focused on the toxicity of saliva to this taxa (e.g., Ghiretti, 1959, 1960; Pilson & Taylor, 1961, but for exceptions see Guer-

Table 5

Crab chelipeds found in 42 intertidal midden piles left by *Octopus dofleini* on Green and Montague Islands, Prince William Sound, AK.

Species	Count found ¹	No. drilled	Avg. size ²
<i>Cancer oregonensis</i> (Dana, 1852)	115 (0.54)	4 (0.03)	1.59 (114)
<i>Lophopanopeus bellus</i> (Stimpson, 1860)	51 (0.24)	4 (0.08)	1.67 (51)
<i>Telmessus cheiragonus</i> (Telesius, 1815)	35 (0.16)	4 (0.11)	2.83 (32)
<i>Pugettia gracilis</i> Dana, 1851	9 (0.04)	2 (0.22)	1.67 (9)
<i>Hapalogaster mertensii</i> Brandt, 1850	3 (0.01)	2 (0.67)	2.57 (3)
<i>Cancer productus</i> Randall, 1839	1 (0.005)	1 (1.00)	4.00 (1)

¹ The number of crab chelipeds found. This does not indicate the minimum number of prey individuals represented in the litter as both left and right chelipeds were usually found in the same midden. Details as in Table 2.

² Size is the mean of cheliped lengths (cm). Details as in Table 2.

ra & Nixon, 1987; Boyle & Knobloch, 1981; Mather & Nixon, 1995; Grisley et al., 1996). Drilling of crustacean prey has been noted for *O. dofleini* (Hartwick et al., 1981) although not described in detail. We found that *Cancer oregonensis*, *Pugettia gracilis*, and *Lophopanopeus bellus* remains were often drilled (10–41% of carapaces, Tables 2–4), whereas bivalve prey and some crabs (e.g., *Telmessus cheiragonus*) were most often not. We found only a single drill mark per prey item regardless of species, in

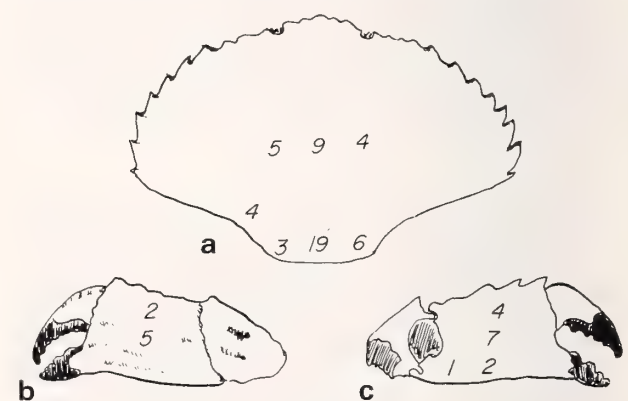


Figure 2

Illustrations of the position and number of *O. dofleini* drills (a) on carapaces of the five most abundant crab species in middens (Table 2), (b) on the outer surface, and (c) inner surface of chelipeds of the same species, plus *Hapalogaster mertensii* (species in Table 5).

contrast to Nixon's (1979) study of *Octopus vulgaris* which found that some species were drilled only once while others were drilled multiple times. Whether this difference is characteristic of the difference in prey (mostly crabs in this study versus gastropods in Nixon, 1979) or of the octopus species remains to be determined. Drilling was not employed preferentially to open the largest prey: *Telmessus cheiragonus* were typically larger than the other crab species, yet were least frequently drilled. The exoskeleton of *T. cheiragonus* is thinner and softer than that of the crabs that were more often drilled (personal observation), and this species probably is easier for the octopuses to pull apart or bite open, techniques that may be attempted in preference to drilling (Hartwick et al., 1981).

Bite marks were previously undescribed and little is known about how octopuses utilize their beaks when capturing prey. *Octopus dofleini* are known to "chip the edges of the (bivalve) shell or break it with their beaks" (Anderson, 1994). We observed bite marks on the largest segment of the leg on a soft-shelled crab species *Telmessus cheiragonus*. The marks were 0.3 to 3.0 cm in length. We could find no data on the size of gape in an octopus. However, using Robinson & Hartwick (1983) we estimated the beak dimensions of a 2.6 kg octopus (the average size of the octopuses that left the middens described in this study). The pigment upper-lateral-wall length (PULWL) was estimated to be 18.8 mm while the total upper-crest length was 30.3 mm. Assuming an octopus' gape would be at most half the PULWL, *O. dofleini* may be able to make bites as large as 9.4 mm and therefore were probably capable of inflicting the marks we describe. In addition, we fed a captive octopus a live *T. cheiragonus* crab and collected the crab remains immediately after feeding. A fresh mark, similar to worn marks found on remains in middens, was found on the penultimate segment of one leg (Figure 1c), confirming that *Octopus dofleini* does make this mark when feeding on *T. cheiragonus*. A captive octopus also left a bite mark on the remains of a *Cancer productus* crab, the first such mark we have seen on remains of any crab other than *T. cheiragonus*.

Descriptions of prey middens have been a primary method of describing octopus diets (Table 1). Despite this reliance, published information on recognizing when remains are left by octopuses is scarce. The composition of midden piles varies from place to place and depends on local habitat as well as other factors (Hartwick et al., 1981; Ambrose, 1984; Vincent et al., 1998), which means that the species that are characteristic of octopus middens must be learned locally. It is not possible to ascribe any single prey remain to a particular cause or process when the remain was found in the absence of an obvious predator and was not marked by the cause of mortality. However, drill marks on one or more items within a midden provide a conclusive indication that the midden contents

were left by a foraging octopus. This definite mark of handling left by octopuses allows the beginning researcher to attribute at least some middens to octopuses and learn what prey are characteristic in a locality. Using a suite of factors, including the association of unmarked items with octopuses in their dens or with items marked by drill holes or bites in the same midden, the researcher can become familiar with prey species that, while locally common in octopus middens, are handled in such a way as to leave no physical marks (e.g., *Chlamys rubida* and *C. hastata* in this study). While some ambiguity will always remain when middens consist only of unmarked items, this local knowledge of how octopuses typically handle each prey species is the only way that the source of such remains can be inferred.

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Morphometric Species Recognition in *Brachidontes darwinianus* and *Brachidontes solisianus* (Bivalvia: Mytilidae)

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Abstract. Shell morphological characters of *Brachidontes darwinianus* and *B. solisianus* were investigated in mussels collected in six areas of sympatry in southeast Brazil. Individuals were measured and analyzed for the relation among shell length, height, and width, as well as other systematic characters used to distinguish the two species. All allometric relations varied according to the site sampled, except the height: length ratio, which consistently separated the two species regardless of where they occurred. Values for this ratio change in distinct shell length classes, and 99% confidence intervals are provided for each length class. Internal and external shell characteristics generally used to separate these species varied both during ontogeny and according to environment. Thus, caution is needed when identifying these species, as single characters may not be useful as taxonomic predictors. Combinations of characters are necessary to separate *B. darwinianus* and *B. solisianus* with more confidence.

INTRODUCTION

The mytilids are represented in Brazil by 12 genera. Among these, the genus *Brachidontes* Swainson, 1840, is the most diverse, with four species divided among three subgenera (Klappenbach, 1965). Mussels belonging to this genus have small lengths (average = 2 cm), sculptured with radial ribs, presenting crenulated margins and short ligaments (Rios, 1995). They are common inhabitants of the intertidal zone of rocky shores and mangroves, forming dominance belts in the ML WN level.

Two species of *Brachidontes* are studied in this work, *B. (Hormomya) darwinianus* (d'Orbigny, 1846) and *B. (Mytilaster) solisianus* (d'Orbigny, 1846). Both species are adapted to stabilize themselves in sites subject to great wave drag forces, presenting a triangular shape, ventral flattening in the antero-posterior plane, and a gregarious way of life (Morton, 1992). *B. darwinianus* occurs from Rio de Janeiro to the northern limit of Patagonia (Avelar & Narchi, 1984a), being most common in estuaries and attached to intertidal rocks at river mouths (Nalesso et al., 1992). Its valves are fan-shaped, sculptured with rounded radial riblets, and with terminal umbones (Rios, 1995). The smaller *B. solisianus* is spread throughout the Western Atlantic coast from Mexico to Uruguay (Rios, 1995). Its shells are inequilateral, rectangular in their posterior edges, sculptured with very fine radial riblets restricted to their posterior ends, and with subterminal umbones

(Avelar & Narchi, 1984b; Rios, 1995). Internally, the two species are distinguished by the position of the median byssal retractor (MBR) muscle scar relative to the ligament. In *B. darwinianus* this scar reaches or extends beyond the ligament, while in *B. solisianus* it never reaches the ligament (Klappenbach, 1965). On the coast of São Paulo state mixed beds of these mussels are frequent.

Because of environmental influences, morphological characters are of low confidence in separating mytilids, presenting high variances as a result of great shell plasticity (Seed, 1968). Variation of shell proportions due to density is also common, as demonstrated by Lent (1967) for *Modiolus demissus* and Brown et al. (1976) for other mytilid species. Nevertheless, it would be very useful to be able to identify species using shell characters. As McDonald et al. (1991) pointed out, to accomplish this goal, "it would be necessary to sample mussels from a wide variety of habitats to determine whether morphometric characters can reliably discriminate among species."

The primary characters used for species distinction within *Brachidontes* also vary according to environmental conditions. Radial ribs, for example, are associated with shell periostracum, being easily lost mainly in adults from sites most exposed to wave action (Klappenbach, 1965). Variation in shell proportion is found in *B. darwinianus*, presenting great phenotypic plasticity in relation to the environment (Nalesso et al., 1992).

As part of a study of succession in intertidal rocky shores of São Paulo, we investigated morphometric characters useful for field identification of the two species of *Brachidontes*. We also tested the congruence of those characters with species diagnoses based on the internal anatomy proposed by Klappenbach (1965), Avelar & Narchi (1984a,b), and Rios (1995).

MATERIALS AND METHODS

Between January and April 1996 samples of sympatric *B. darwinianus* and *B. solisianus* were collected from five rocky shores in São Paulo State, southeastern Brazil: Milionários (23°58'S, 46°22'W); Barequeçaba (23°50'S, 45°26'W); Lagoinha (23°31'S, 45°11'W); Dura (23°30'S, 45°S10'W), and Lázaro (23°31'S, 45°08'W). Further samples of *B. solisianus* were collected from four additional sites: Cigaras (23°44'S, 45°24'W, State of São Paulo); Rasa and Saquarema (22°44'S, 45°24'W and 22°55'S, 42°31'W, respectively, State of Rio de Janeiro), and Pina (8°S, 35°10'W, State of Pernambuco).

For initial species separation of *B. solisianus* and *B. darwinianus* we relied upon defined characteristics of overall shape (fan or elongated) and sculpture patterns. Mussels were sampled selectively for the whole length range in their dominance zone along each site. Maximum length, width, and height of all animals were measured to the nearest 0.1 mm with vernier calipers. The angle formed by the ligament margin and the ventral axis was estimated to the nearest 5° using a graded angular scale. The valves were opened and the inner side of the right one was examined under a stereoscopic microscope. The distance separating the anterior edge of the median byssal retractor (MBR) scar to the posterior end of the ligament was measured to the nearest 0.001 mm (Figure 1). When the scar passed the resilium, a negative value was attributed. The presence and position of the demibranch retractor scar (linked or not to the MBR scar) was also noted. When this scar was not markedly visible on the valve, it was registered as absent. To eliminate size effects, *B. darwinianus* individuals larger than 20 mm were not used for comparisons of taxonomic characters.

Our purpose while studying morphometric relationships was to find out an objective form to distinguish the two species. For this reason, we investigated attributes that could be linked to general shell shape and express differences in the allometry of *B. darwinianus* and *B. solisianus*. Morphometric relations were studied fitting each pair of variables X and Y to the allometric equation, using least squares regression:

$$\log Y = a + b \log X$$

where a and b are constants (Seed, 1980). Species and localities were compared using analysis of covariance (ANCOVA), according to the following model:

$$Y_{ij} = S_i + L_j + S_i * L_{ij} + C + S_i * C + \epsilon$$

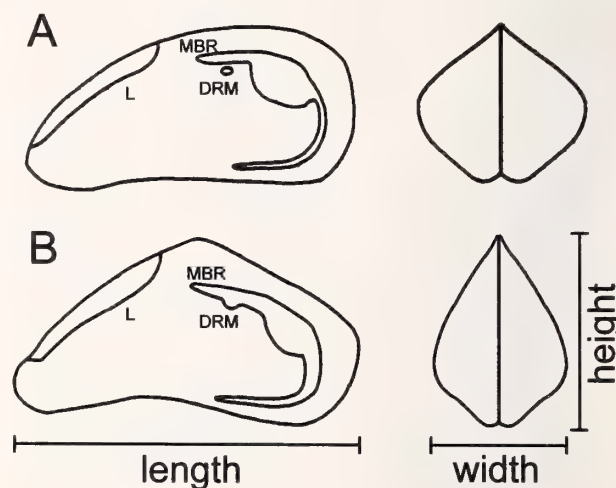


Figure 1

Morphological shell characters analyzed in this study. A. *Brachidontes darwinianus*. B. *Brachidontes solisianus*. Abbreviations: L, ligament; MBR, mean retractor muscle scar; DRM, demi-branch retractor muscle scar.

where S_i denotes species i , L_j the locality j effect, C is the covariable being analyzed and ϵ the experimental error (Draper & Smith, 1981). As our goal was not to study differences among different localities, we searched for relations that were constant across sites with different hydrodynamic forces. Thus, when the interaction term ($S_i * L_{ij}$) was significant, the relation analyzed was not considered a good taxonomic predictor, as its effect within a species would depend on the beach where the sample was collected.

Separate variables studied were analyzed using a two-way ANOVA (Underwood, 1981). For all linear models, assumptions of normality and homogeneity of variances were tested by plotting the residuals against the estimated values. These were visually inspected to detect trends due to violations of the assumptions or any pattern not considered by the models (Box et al., 1978).

To analyze variation of the muscle scars, observations were pooled within length classes determined by 5 mm intervals of shell length. Presence of the demibranch scar was analyzed in these classes using log-linear models in a three-way contingency table (Agresti, 1990). In this analysis, the model being analyzed lacks one of the variables of interaction terms, and is tested against the saturated model (with all variables and interaction terms possible). In this way, it is possible to test the significance of each interaction term. If the interaction is significant, the main effects are also significant, as log-linear models are hierarchical (Agresti, 1990). The model with the least number of variables and interactions that does not significantly differ from the saturated model is the best one to describe the data (Agresti, 1990). Thus, it was possible

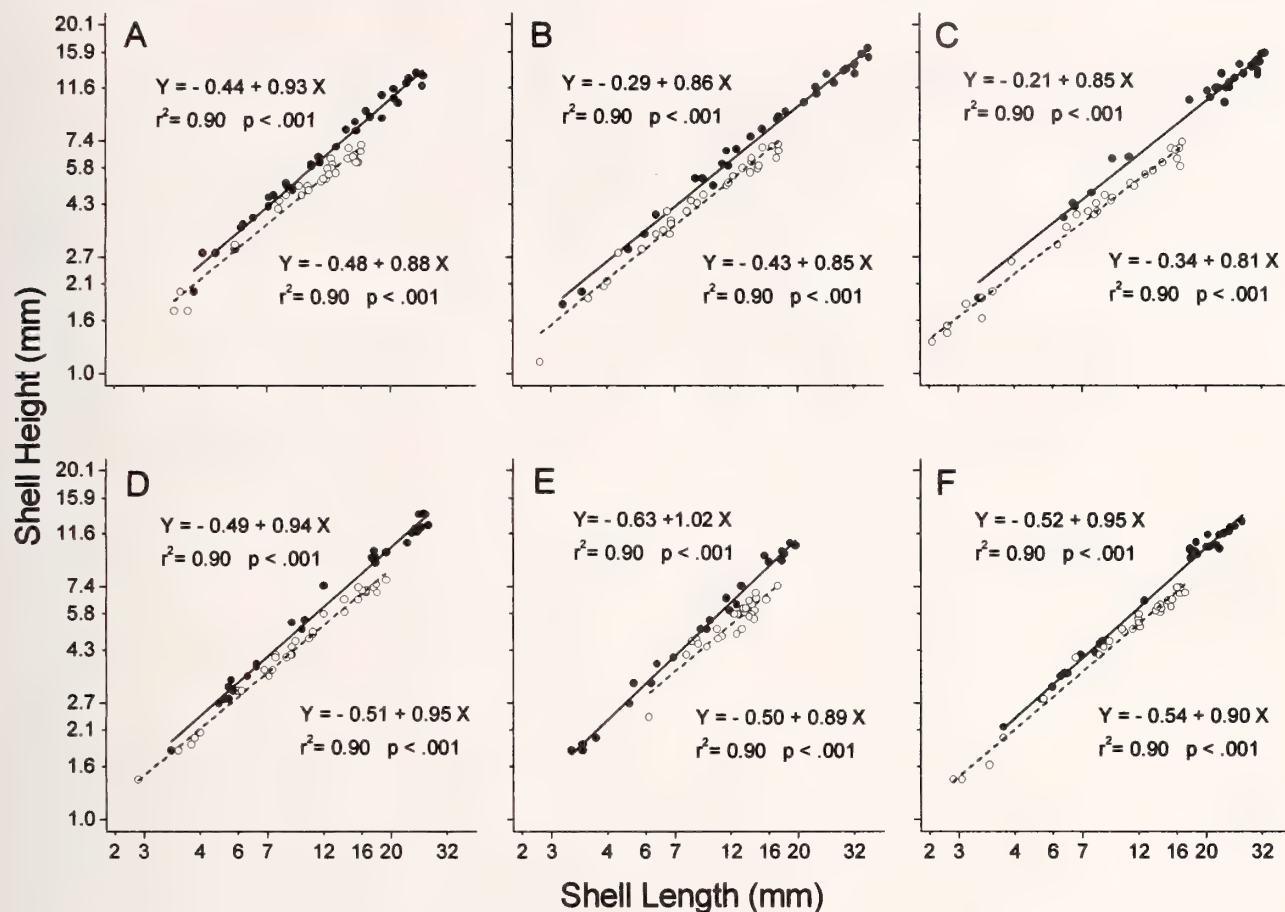


Figure 2

Shell height and length relations for *B. darwinianus* (solid circles, solid lines) and *B. solisianus* (open circles, dashed lines) within the sites sampled: A. Barequeçaba, B. Dura, C. Lagoinha, D. Lázaro, E. Milionários, F. Soares. Specific equations for each relation are presented. Numbers in parenthesis are standard errors for the determination coefficients. All values are plotted in logarithmic scale.

to test if the position or presence of these scars were dependent on the species considered, or on the shell length of the animal. All individuals of each species were grouped, as a preliminary survey did not show any pattern among localities. All analyses were done with SYSTAT software (Wilkinson, 1990).

RESULTS

Analysis of residuals did not detect violations of the assumptions made on the linear models used. Our results indicate a great variation of shell characters, with great overlap of shell proportions in the smaller length classes.

Shell length was extremely variable among beaches: *B. darwinianus* varied from 3.0 to 36.0 mm, while *B. solisianus* ranged between 2.2 and 20.0 mm. *B. darwinianus* had higher and wider valves than *B. solisianus*, varying from 1.8 to 16.3 mm in height and 0.1 to 12.2 mm in

width, while *B. solisianus* showed height between 0.3 to 7.9 mm and width from 0.1 to 9.2 mm. The relationship between shell height and length was linear in both species (see values for regression coefficients in Figure 2). This relation was determined only by species, without any interaction with sampling sites (Table 1). The slopes differed significantly ($P < 0.001$), with *B. darwinianus* increasing faster in height than *B. solisianus* of the same shell length (Table 1). This means that the regression lines for the two species cross, and for individuals with shell lengths smaller than 5 mm the values for relative height may overlap. Nevertheless, height: length ratio separates both species (Figure 3). Values for this ratio, however, depend on the relative shell length of the individuals; *B. darwinianus* maintains fairly constant values at small lengths, decreasing as the individuals attain larger shell lengths, while *B. solisianus* rapidly decreases this value.

Table 1

Analysis of covariance for shell relations between *B. darwinianus* and *B. solisianus*; the underlined variable is the dependent one being tested in the ANCOVA model.

Source	ANOVA			
	DF	Sum of squares	F	P
Height $r^2 = 0.99$				
Localities	5	0.052	2.060	0.070
Species	1	0.003	0.666	0.415
Localities*Species	5	0.009	0.339	0.889
Length	1	86.475	17,234.886	<0.001
Length*Species	1	0.082	16.317	<0.001
Error	345	1.731		
Width $r^2 = 0.98$				
Localities	5	0.764	16.868	<0.001
Species	1	0.076	8.390	0.004
Localities*Species	5	0.385	8.496	<0.001
Length	1	105.716	11,668.061	<0.001
Length*Species	1	0.226	24.965	<0.001
Error	344	3.117		
Width $r^2 = 0.96$				
Localities	5	0.520	7.424	<0.001
Species	1	0.001	0.048	0.826
Localities*Species	5	0.412	5.881	<0.001
Length	1	103.160	7,362.554	<0.001
Length*Species	1	0.533	38.021	<0.001
Error	344	4.820		

Both patterns illustrate the changes in the slope of the untransformed relation between height and length, but within the length classes where both species overlap (0–20 mm), the 99% confidence intervals for each length class indicate a clear separation (Table 2), except for the 0–5 mm length class.

Shell width and length were positively correlated in both species (Figure 4), but a significant interaction between species and sites was detected (Table 1). This means that differences observed for the two species were dependent on the site considered. Nevertheless, *B. solisianus* seems to become thicker more frequently than *B. darwinianus*, in individuals greater than 10 mm. *B. darwinianus* tended to have taller and narrower shells than *B. solisianus*, but this was also site-related (see analysis for Width \times Height in Table 1). In one site (Soares) the relation was weak for *B. darwinianus*, with greater variation within shorter individuals.

The angle formed by the ventral margin and the ligament showed a great variation both within species (according to shell length) and among beaches, with strong interaction between species and localities (Table 3), and was a poor predictor to distinguish between the two species. Nevertheless, as a general trend, *B. darwinianus* individuals exhibited greater angles between shell margins,

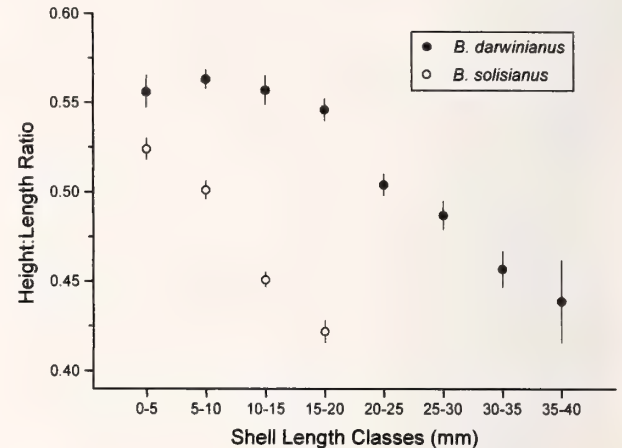


Figure 3

Mean values (\pm SE) of the height:length ratio for *B. darwinianus* (solid circles) and *B. solisianus* (open circles) along 5 mm length classes.

as indicated by their ranges (*B. darwinianus*: 30–60°; *B. solisianus*: 15–55°).

The distance from the median byssal retractor scar to the ligament varied with shell length in *B. darwinianus* (Figure 5). In individuals smaller than 15 mm, this scar scarcely passed the ligament, while in larger individuals the scar extended beyond the ligament, but there was a great variation within this character. Conversely, in *B. solisianus* the position of the scar almost never reached the ligament, irrespective of shell length (Figure 5), but this species includes only the smaller length classes found in *B. darwinianus*; thus, individuals from the same size can

Table 2

Analysis of variance for the height:length ratio along different length classes smaller than 20 mm, and 99% confidence intervals for the ratio, showing dependence on length classes for *B. solisianus*.

Source	ANOVA			
	DF	Sum of squares	F	P
Length class	3	0.118	332.72	<0.001
Species	1	0.367	35.62	<0.001
Length class*Species	3	0.068	20.65	<0.001
Error	287	0.317		

Length classes	<i>B. darwinianus</i>		<i>B. solisianus</i>	
	Lower 99%	Upper 99%	Lower 99%	Upper 99%
0–5	0.533	0.579	0.509	0.539
5.1–10	0.550	0.576	0.488	0.514
10.1–15	0.536	0.578	0.441	0.461
15.1–20	0.531	0.561	0.407	0.437

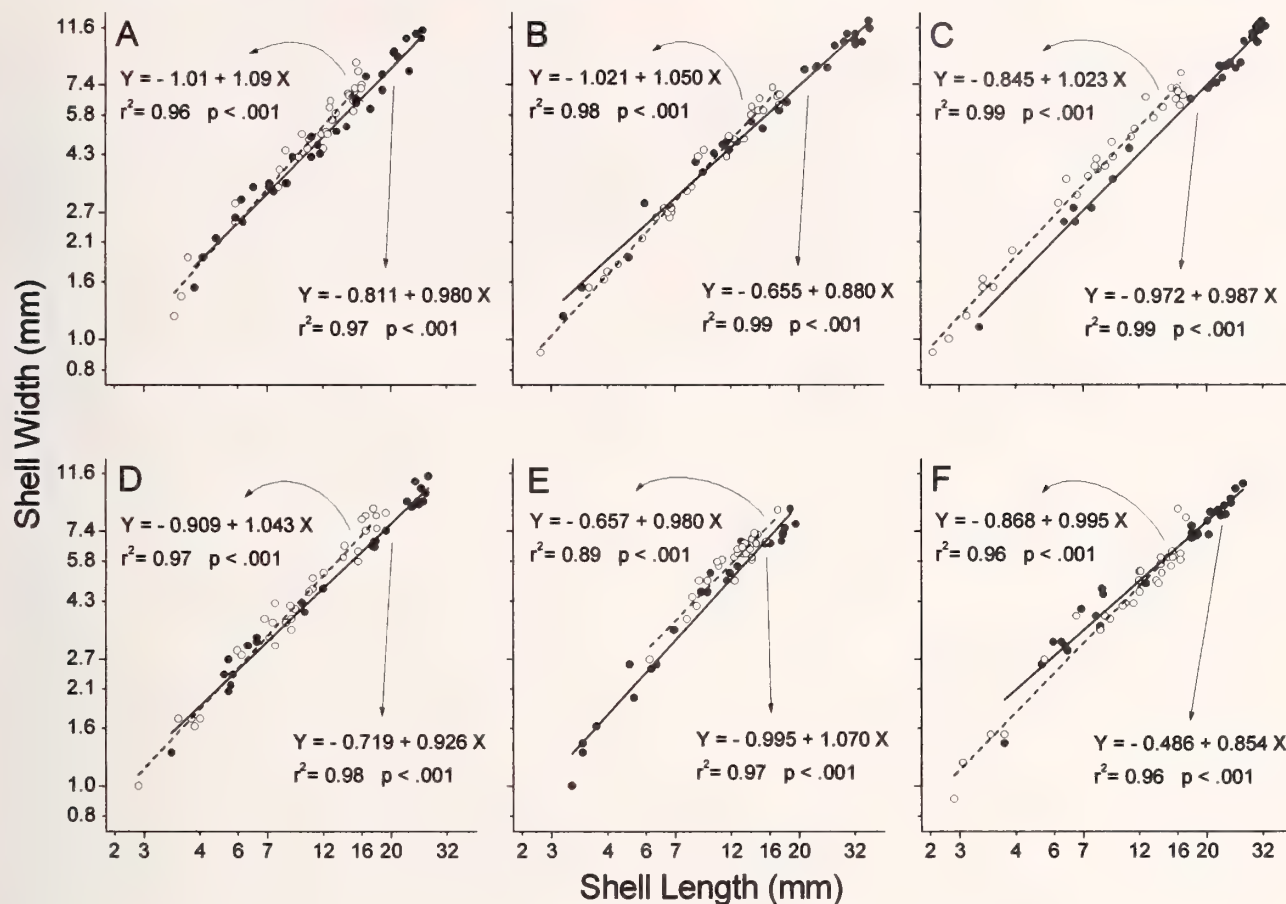


Figure 4

Shell width and length relations for *B. darwinianus* (solid circles, solid lines) and *B. solisianus* (open circles, dashed lines) within the sites sampled. Conventions as in Figure 2.

be wrongly assigned to one of the species, if only this character is used. Specimens from the other sites (Cigaras, Pina, Rasa, and Saquarema) showed the same patterns.

Log-linear analysis for the presence of the demibranch retractor muscle scar showed that there is conditional independence between the presence of this scar and the length classes, depending on the species (Table 4). The fitted model was

$$\ln \hat{f}_{ijk} = \mu + \alpha_i + \beta_j + \gamma_k + \alpha\beta_{ij} + \alpha\gamma_{ik}$$

where α_i is the effect of the species i , β_j is the effect of the length class j , and γ_k is the response variable, referring to the position k of the demibranch scar (present or not in the shell) (Likelihood Ratio Chi-Square = 5.26, df = 6, $P = 0.511$). This means that the chance of detecting a scar depends on the shell length of the individual. Both effects were significant, but there was no interaction between them (they are independent). These effects were different for the two species: in *B. darwinianus* this scar

is almost always present, independent of shell length. In *B. solisianus* almost 40% did not present this scar, with a greater chance of not detecting the scar at all depending on the length class considered.

When present, the position of the demibranch scar did not depend on the species or on the length class examined. The final fitted model for these three variables was

$$\ln \hat{f}_{ijk} = \mu + \alpha_i + \beta_j + \gamma_k + \alpha\beta_{ij}$$

(Likelihood Ratio Chi-Square = 11.21, df = 7, $P = 0.13$). Although there was an interaction between species and length classes, there was no influence of these factors on the position of the demibranch scar, whether linked or not to the MBR scar.

DISCUSSION

Traditional morphological characters frequently applied in the taxonomy of the species within the genus *Brachidontes* proved to be inconstant over a wide shell length range in this study.

Table 3

Mean values for the angle formed by the ventral margin and the ligament and analysis including only sites with both species. Individuals from different length classes were pooled, as not all classes were present in the sites studied.

	<i>B. darwinianus</i>		<i>B. solisianus</i>	
	Mean (std. err.)	Range	Mean (std. err.)	Range
Barequeçaba	44.1 (0.7)	35–55	36.0 (1.3)	25–55
Dura	38.5 (0.8)	30–45	30.5 (1.0)	20–40
Lagoinha	42.5 (0.8)	30–50	32.5 (1.0)	15–40
Lázaro	45.2 (1.3)	35–60	37.0 (0.9)	30–50
Milionários	39.0 (1.7)	30–60	32.5 (1.2)	20–45
Peres	40.3 (0.9)	30–50	37.9 (0.9)	30–45
Cigarras			33.3 (1.6)	15–45
Pina			33.6 (1.0)	25–45
Rasa			34.5 (1.3)	25–50
Squarema			33.7 (1.2)	20–45

ANOVA				
Source	DF	Sum of squares	F	P
Localities	5	1,938.567	11.869	<0.001
Species	1	4,585.677	140.381	<0.001
Localities*Species	5	500.917	3.067	0.010
Error	345	11,269.758		

Individuals of the species studied showed maximum adult length similar to specimens collected in other sites (Klappenbach, 1965; Avelar & Narchi, 1984a; Nalesso, 1988; Rios, 1995). In these studies, *B. darwinianus* attained a maximum length of 33 mm, while *B. solisianus* reached a maximum length of 20.1 mm. The sites where we found *B. darwinianus* individuals with greatest shell lengths had the widest distribution of this species in relation to *B. solisianus*. The former species is found covering the inferior intertidal zone, while *B. solisianus* is distributed upper in the intertidal (Nalesso, 1988; Tanaka, unpublished data). In the other beaches *B. darwinianus* is more restricted, occupying patches related to the presence of fresh water flow, or in low proportions of mixed species beds.

All allometric relations examined varied according to the species and locality considered. Individuals of *B. darwinianus* become higher within the same length variation of *B. solisianus*, with shells also becoming more curved. This character varied consistently among the species and the shores sampled, without interaction between them. Seed (1968) showed that in *Mytilus edulis* shells tend to grow taller and become more curved as individuals attain their maximum length, or when the animals occur in dense populations. This pattern seems to occur in *B. darwinianus*, as this species can reach high densities due to

the secondary substratum formed by the mussel bed: recruitment can occur over the adult individuals, and young mussels can be found with their byssus attached to the shells of the older ones (Tanaka, unpublished data).

The best taxonomic character we could find using morphometric relationships was the height: length ratio. Although at the smallest length class this ratio may overlap (Table 2), this may only reflect similar shell characteristics within post-recruited individuals and a greater plasticity in adults (Seed, 1980). Larger individuals can be readily separated with 99% of confidence using the values calculated.

In the smallest length classes, a good taxonomic predictor is the presence of radial ribs over all the shell surface in *B. darwinianus*, while in *B. solisianus* these ribs are present only in the shell posterior margin. The number of ribs in *B. darwinianus* varies depending on the salinity conditions (Nalesso et al., 1992): individuals grown next to rivers present fewer ribs than individuals growing in the sea. In exposed shores, shells are also more eroded, making it more difficult to distinguish very young individuals of the two species.

Greater angles between shell margins were also used by Avelar & Narchi (1984a,b) to distinguish *B. darwinianus* from *B. solisianus*. They proposed a value around 40° for *B. darwinianus* and 30° for *B. solisianus* and stated that those values differ for specimens of the same size. We have not found consistency in this character because it exhibited great variation related to shell length, as well as to sample location.

The position of the median byssal retractor scar is not a consistent character to separate the species studied. Klappenbach (1965), however, used this character to separate *B. exustus* and *B. solisianus* from *B. rodriguezi* and *B. darwinianus*. In the latter two species, the scar reaches or extends beyond the ligament, while in the former it falls short of the ligament edge. Within *B. solisianus* the scar does not reach the ligament, and the distance is constant independent of shell length (see Figure 5). In *B. darwinianus* samples, the scar approaches the resilium as the animal grows, passing it when the shell reaches 15–20 mm. According to Klappenbach (1965), *B. exustus* presents terminal umbones, while *B. darwinianus* has subterminal ones. Two subspecies have been described for *B. darwinianus*, based on the position of the MBR scar: *B. d. darwinianus* (with thin radial ribs, MBR scar surpassing the ligament) and *B. d. mulleri* (with thicker radial ribs, MBR scar only just reaching the ligament). Our data does not support the subdivision of this species based solely on shell characteristics, as they may vary both during the ontogeny of the individuals and according to environmental forces. Although there is a great variation in *B. darwinianus*, the length of this scar seems to be related to animal size, and in both species individuals smaller than 20 mm present similar scars.

Avelar & Narchi (1984a, b) suggested that the position

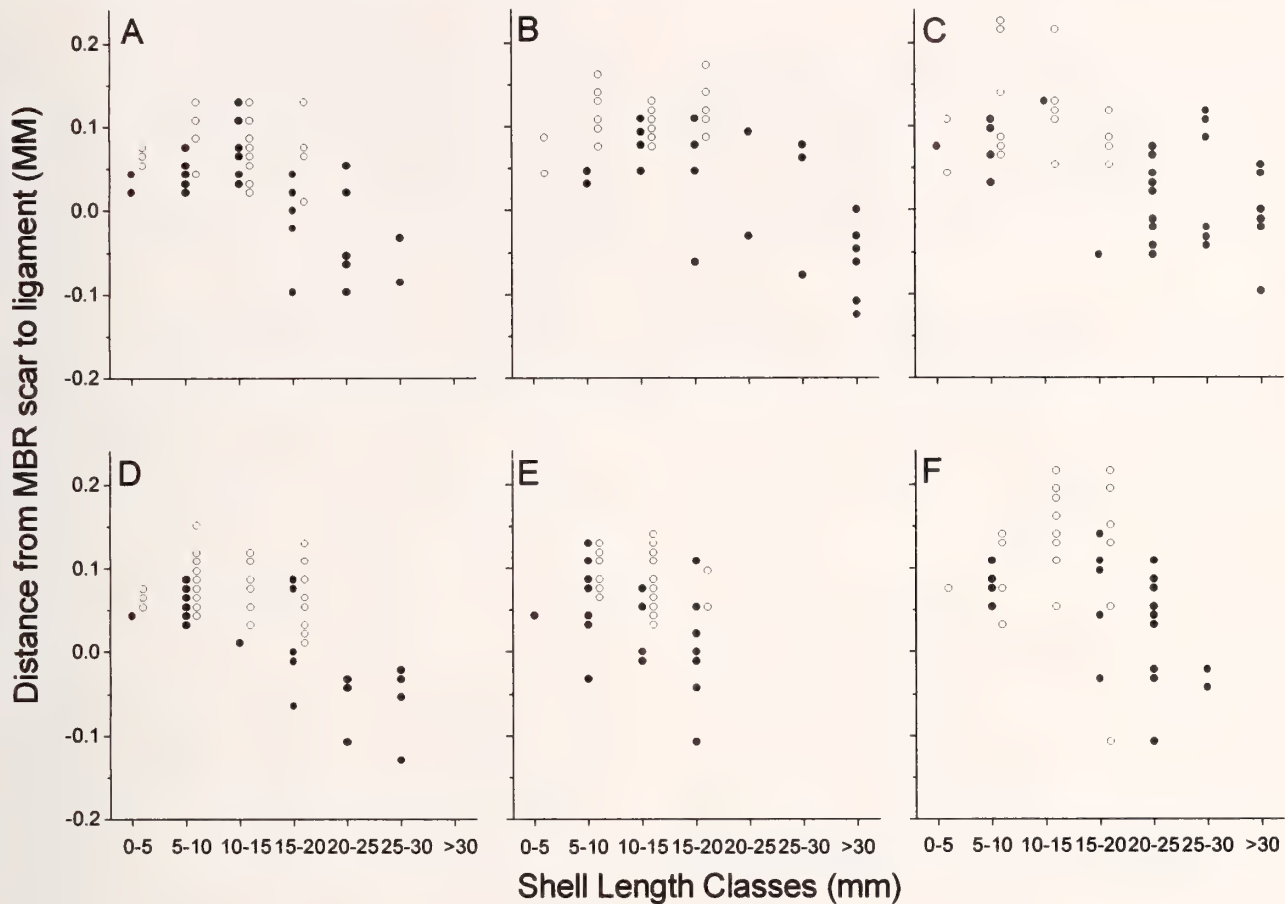


Figure 5

Values of the distance from MBR scar to ligament against shell length classes for *B. darwinianus* (solid circles) and *B. solisianus* (open circles) within the sites sampled: A. Barequeçaba, B. Dura, C. Lagoinha, D. Lázaro, E. Milionários, F. Soares.

of the demibranch retractor muscle scar could be useful to separate *B. darwinianus* and *B. solisianus*. However, we found no differences in the position of the scar either between species or among shell length classes. Therefore, no taxonomic value can be assigned for this character. On the other hand, our results show that in *B. darwinianus* this scar is almost always present, while in *B. solisianus* a great proportion of shells examined presented no scars at all.

This study revealed a great plasticity of shell characters in species of the genus *Brachidontes*. Such variability was also reported for *Mytilus edulis* by Seed (1968). He emphasized that in species with planktonic development the uncertainty of the recruitment site favors wide phenotypic expression. Phenotypic plasticity is adaptive for organisms inhabiting unpredictable sites and/or with wide geographical range (Brown, 1985; Etter, 1988). These apply to the species of *Brachidontes* studied, because of the existence of a planktonic dispersal phase. Morphological characters like shell sculpture and geometry are frequent-

ly complex and usually determined by many loci that can themselves be polymorphic (Berger, 1983). Species with wide dispersal capacity are exposed to a great range of different habitats in a heterogeneous environment (Janson, 1987). As a consequence, for such cases, Grassle & Grassle (1978) suggest that individuals presenting a great degree of variation in genetic loci related to adaptive characters are favorably selected. McDonald et al. (1991) stated that allozyme characters should be the primary means of distinguishing among species of the genus *Mytilus*. This may also apply for other mussels such as *Brachidontes*. Genetic studies in *Brachidontes* would be very useful to clarify the distinction among species and the selective mechanisms that determine species form and distribution. For ecological purposes, recruits of the two species are not distinguishable using shell characteristics, but the height: length ratio forms a strong character for species discrimination between *B. darwinianus* and *B. solisianus* adults.

Table 4

Frequencies of shells with the demibranch retractor scar linked or not to the median byssal retractor scar. For *B. darwinianus* only shells with length smaller than 20 mm were considered; there was no difference among the position of scars in longer shells.

Species	Length class (mm)	Position of scar		
		Present		Absent
		Linked	Separated	
<i>B. darwinianus</i>	0–5	2	3	0
	5–10	18	26	1
	10–15	13	5	0
	15–20	18	13	0
<i>B. solisianus</i>	0–5	4	3	7
	5–10	20	13	14
	10–15	29	11	33
	15–20	13	8	12

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Early Development of *Fissurella picta* (Gmelin, 1791)

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Abstract. The early stages of the embryonic and larval development of the limpet *Fissurella picta* (Gmelin, 1791) (“lapa”) are described. The period after fertilization and until the initial trochophore stage at 10°C was 74 hr. The principal characteristic of the embryonic development is the presence of a gelatinous coat. Routine methods of spawning induction did not produce positive results.

The results suggest that in spite of some critical events, it is possible to obtain larvae until the early trochophore stage under laboratory culture conditions, which marks significant progress in cultivating this species, given the intense exploitation and the high commercial value of the “lapa.”

INTRODUCTION

In spite of the growing commercial importance of species of the genus *Fissurella* (locally referred to as “lapa”) in Chile (Bretos et al., 1988a; Oliva & Garrido, 1994), little is known about its embryonic and larval development. The knowledge of early life stages is fundamental to the evaluation of the feasibility of cultivation of species of this genus. The breeding cycle of *Fissurella picta* will be reported (Pérez et al., in preparation).

The aim of this study was to evaluate spawning and fertilization under artificial conditions, as well as to describe the early development of *F. picta* (Gmelin, 1791), which is one of the principal “lapas” species from southern Chile (Bretos et al., 1988b).

MATERIALS AND METHODS

During the period of maximum gonadic maturity (July), specimens of *Fissurella picta*, measuring over 5 cm, were taken from the rocky intertidal zone of Metri Bay, southern Chile (41°36'S, 72°42'W). Epibionts were removed and the specimens of *F. picta* were maintained in the laboratory for an acclimation period of 20 days. Fifteen animals were placed in an aquarium at 10°C, 32‰ salinity, with a constant air supply, and fed *ad libitum*, to increase chances of spontaneous spawning, according to the methodology described by Giese & Pearse (1974).

The following alternative methods of inducing spawning were also tested (15 specimens for each treatment): (a) **thermal shock**: animals were maintained for 4 hr at a temperature of 5°C, and subsequently transported to a thermoregulated bath at a temperature of 24°C; (b) **electric shock**: electric current from a 6V battery was applied to specimens maintained in seawater; (c) **osmotic shock**: specimens were injected in the siphon with KCl 0.5 M.

In addition, gametes, obtained by dissection of 15 specimens, were subsequently rinsed in filtered seawater (1

µm), and then fertilized using 15–17 sperm for each oocyte. Oocytes were rinsed after fertilization with sterile, filtered seawater (1 µm), and maintained in the dark at 10°C, with a constant air supply, and water change every 2 days during the entire period of development.

RESULTS

Specimens acclimated in the laboratory and fed *ad libitum* spawned (eggs and sperm) spontaneously into the seawater. The release of oocytes and sperm through the apical hole of the shell indicates that external fertilization occurs in *Fissurella picta*.

Two- and 4-cell embryos were first observed after 3–4 hr of fertilization; they continued to develop to the trochophore stage within the egg shell after 72 hr (Table 1). The artificial spawning induction methods tested (thermal, electric, and osmotic shock) did not produce positive results.

From the second half of July to the end of August (wintertime), coincident with the period of maximum maturity, we found mobile sperm in dissected gonads. At this time the oocyte gelatinous coat became less dense when rinsed in seawater. This enabled the sperm to penetrate through the micropile, into the interior of the oocyte, resulting in fertilization. After 15 to 20 min, immediately after fertilization, a series of changes occurred in the oocytes. A palear zone was produced in the cytoplasm of the oocyte; in this area, 1 hr later, the polar corpuscle was eliminated (Figure 1a; Table 1). Two hours later segmentation began, which occurred, in its entirety, within the capsule which encases the oocyte. Initially blastomeres were produced. At this stage the polar corpuscle was still present (Figure 1b), followed by the 4-cell embryo (Figure 1c; Table 1). The 8-cell embryo presented macromers and micromers (Figure 1d). Approximately 12 hr after fertilization, the blastula stage was

Table 1

Post-fertilization period stages and timing of early development in *Fissurella picta* at 10°C, 32‰ salinity.

Event	Period after fertilization (hours)
Elimination of polar corpuscle	1
2-cell embryo	2
4-cell embryo	3-4
Blastula	12
Gastrula ciliate within the egg shell	19
Initial trochophore in egg shell	72
Length of trochophore swimming	96
Length of maintenance in culture until trochophore dead	144

reached and after 19 hr, the ciliate gastrula was observed, rotating within the capsule, (Figure 1e). After 72 hr, the initial trochophore stage was observed (Figure 1f). The trochophore had an anterior ring of large cilia in constant motion, producing continuous larval rotation within the capsule.

DISCUSSION

The results described here show that the artificial routine methods for spawning did not produce positive results. Spawning and fertilization are possible under laboratory conditions in mature specimens of *Fissurella picta*. In mature specimens maintained in the laboratory under the conditions described in Materials and Methods, spontaneous spawning occurred. Gametes could be obtained by gonad dissection. Nevertheless, the best results were achieved by maintaining specimens in the laboratory until spontaneous spawning occurred. However, there are problems that must be overcome before culture can be carried out on a larger scale, i.e., larval development until metamorphosis.

Ward (1966) reported oocytes with a gelatinous coat in species of the genus *Fissurella*. In Chilean species of venerids this has been described (Padilla, 1983; Guerra et al., 1994) where artificial fertilization was possible only under special conditions, such as osmotic shock (Padilla & Olivares, 1986). In spite of this, the components of this gelatine have been associated with the induction of acrosomal reaction (Epel, 1975). During periods of maximal maturity in *F. picta*, rinsing the eggs in seawater was sufficient to obtain fertilization of oocytes. In fact, the loss of gelatinous coat and subsequent fertilization occurred spontaneously in the experimental aquaria.

The early trochophore is lecithotrophic, and may reduce early mortality. Lewis (1960) studied trochophore larvae with a short pelagic lifespan in other species of the genus, such as *F. barbadensis* Gmelin. Similarly, trochophores and veliger larvae that go through gelati-

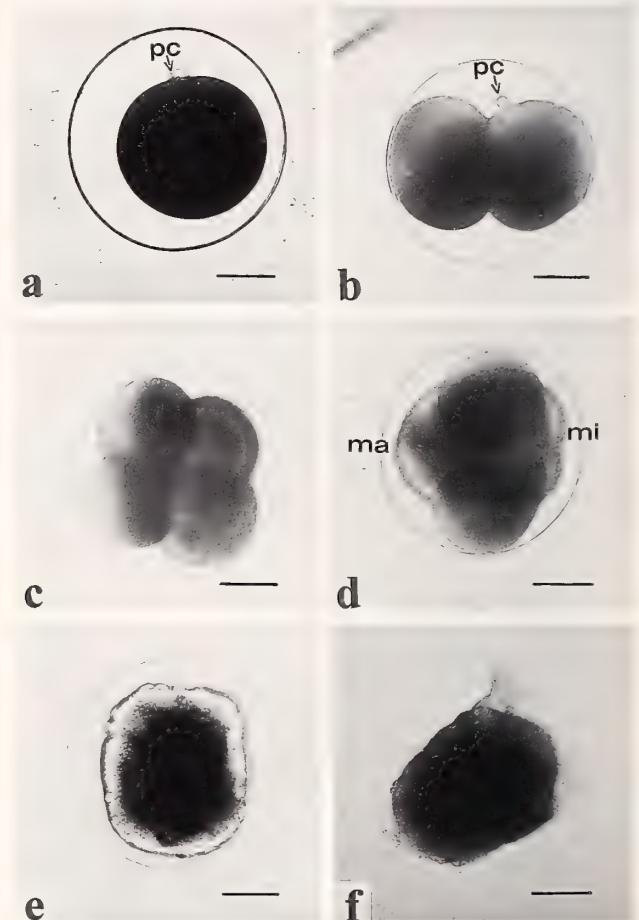


Figure 1.

a. Post-fertilization stages and early development in *Fissurella picta* at 10°C and 32‰ salinity: the polar corpuscle (pc) is eliminated; b. the first segmentation, formation of two blastomeres with polar corpuscle (pc); c. the 4-cell embryo; d. the 8-cell embryo with macromeres (ma) and micromeres (mi); e. the ciliate gastrule with rotatory movement at the interior of capsule; f. trochophore larvae scale bars = 50 μ m.

nous mass enveloping ovocytes and emerge as miniature adults have been reported in *Diadora apertura* (= *F. reticulata*) (Boutan, 1886 in Ward, 1966)). Data for *F. picta* would indicate that it follows an intermediate pattern, between these two types of development in spite of the fact that the length of the trochophore stage and timing of metamorphosis are not known.

Given the intense exploitation and the high commercial value of the "lapa" species in Chile (Bretos, 1988a), basic information must be obtained to evaluate the feasibility of intensive cultivation. Our results suggest that it is possible to obtain larvae until the early trochophore stage, under artificial conditions.

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NOTES, INFORMATION & NEWS

Occurrence of the Asian Clam *Corbicula fluminea* (Müller, 1774) (Bivalvia: Sphaeriacea: Corbiculidae) in Colorado

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The invasive pest species, the Asian clam *Corbicula fluminea* (Müller, 1774) (Bivalvia: Sphaeriacea: Corbiculidae), was first reported in the United States in the Columbia River, Washington, in the 1930s (Britton & Morton, 1982). Since that time it has spread across the country into at least 35 states (Counts, 1986; McMahon, 1983). The success of this species in colonizing North American fresh waters is mainly due to its high fecundity, high growth rate, and quickly settling, free-living larval stage (McMahon, 1983). In addition, its great adaptability to disturbed environments has allowed it to infest these areas quickly. Possible limitations to its dispersal are speculative but include low water temperatures (French & Schloesser, 1991, 1996; Graney et al., 1980; Mattice & Dye, 1976; McMahon, 1983); exposure during low water (McMahon, 1983); reduced phytoplankton as a food source (French & Schloesser, 1996); low pH, causing shell dissolution (Kat, 1982); overpopulation resulting in massive die-offs (Sickel, 1986), and competition with zebra mussels *Dreissena polymorpha* (Pallas, 1771) (Hebert et al., 1989; Nalepa & Schloesser, 1993).

In the United States *Corbicula fluminea* currently ranges as far north as the Great Lakes (Clarke, 1981; Counts, 1986; French & Schloesser, 1991, 1996; Scott-Wasilk et al., 1983) and Washington (Britton & Morton, 1982; Counts, 1986), although it has not yet invaded the New England states (Counts, 1986). Southern distribution occupies all southern states including the southern tips of Texas and Florida (Counts, 1986; McMahon, 1983). *C. fluminea* was first reported in the Platte River as dead shells in Lancaster and Dawson Counties, Nebraska (Freeman & Perkins, 1992). However, Peyton & Maher (1992, 1995) found living populations soon after. Neighboring Kansas has populations along the Kansas River drainage and one population on the North Fork of the Ninescaw River (Arkansas River drainage) (Counts, 1991). In 1993, *C. fluminea* was first discovered in neigh-

boring Colorado in Cherry Creek Reservoir, Arapahoe County (Figure 1), part of the Platte River drainage (Nelson & McNabb, 1994). Since then, Crane et al. (1996) found the species in Highline Lake, Mesa County (Figure 1), in the western part of the state far removed from the Cherry Creek population. Kreiser & Mitton (1995) speculated that *C. fluminea* could be adapting to colder climates without the benefit of apparent thermal refuges such as power plants, despite high winter mortalities. Previously, it had been reported that severe cold causes heavy mortality in the species (French & Schloesser, 1991, 1996) especially at temperatures below 2°C (Mattice & Dye, 1976).

We wish to report on the distribution of *Corbicula fluminea* in Colorado, including several new localities, all in areas that experience temperatures below 2°C, indicating it can survive and reproduce in colder climates.

In 1996, while surveying freshwater mussels along the Arkansas River drainage in Colorado, Cordeiro observed three previously unreported populations of *Corbicula fluminea* in Queen's Reservoir, in the Arkansas River below the dam of John Martin Reservoir, and in Pueblo Reservoir (Figure 1). MacWilliams surveyed the perimeter of Pueblo Reservoir in November 1996, by canoe and on foot, to determine the approximate density and substratum for *C. fluminea* at that location.

Queen's (Neeskah) Reservoir is a small pond located 5.5 miles north and 5.25 miles east of Big Bend at an elevation of 3875 feet in Kiowa County. It is part of the Colorado State Park System. In Queen's Reservoir, Cordeiro found three intact, empty shells plus 30 valves in July 1996. Shell length ranged from 13.8 to 32.5 mm (mean 26.75 mm, $n = 33$). All the exposed specimens were found at least 10 meters above the water line. The reservoir had receded considerably from the high water mark where bottom sediment was coarse sand to a point where bottom sediment was a very fine, silty, thick mud. The clams were all found on the exposed sediment 10 meters or more from the receded water line, beneath which was black mud. The sandy sediment where the clams were found was less than 12 cm deep atop a much deeper layer of dried mud. Prolonged searching for several hours revealed no living specimens or dead shells underwater or less than 10 meters from the water's edge.

In October 1996, Cordeiro discovered a second population west of Queen's Reservoir in a pool of the Arkansas River below the dam to John Martin Reservoir, Bent County. Six valves and five living specimens were collected. The species is reportedly surviving in John Martin

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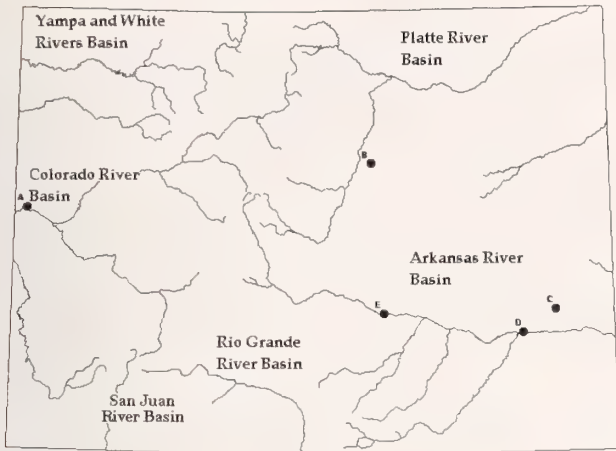


Figure 1

Distribution of *Corbicula fluminea* (Müller) in Colorado. Closed black circles designate localities where *C. fluminea* has been collected in Colorado. A = Highline Lake, Mesa County, summer 1995 (Crane et al., 1996). B = Cherry Creek Reservoir, Arapahoe County, June 1993 (Nelson & McNabb, 1994). C = Queen's Reservoir, Kiowa County, July 1996 (present study). D = Arkansas River at John Martin Reservoir, Bent County, October 1996 (present study). E = Pueblo Reservoir, Pueblo County, November 1996 (present study).

Reservoir (Dr. Scott Herrmann, University of Southern Colorado, personal communication, August 1996).

In August 1996, Cordeiro and MacWilliams found *Corbicula fluminea* in Pueblo Reservoir at Lake Pueblo State Park, Pueblo County, surviving in relatively great numbers. Several individuals were observed in the sandy beach sediment. Few dead shells and many small individuals of less than 5 mm were noted, suggesting that the population is healthy.

Samples of the Pueblo Reservoir population were collected in November 1996 using a drag net sampler (width 0.305 m) according to the method of Britton & Morton (1982). Individual clams were counted and measured for length with vernier calipers to the nearest millimeter and sorted into three size categories: < 6 mm, 6–13 mm, and 14–27 mm. Clams less than 4 mm were difficult to see within the sample and time-consuming to sort in the field; therefore, the smaller category reflects mainly clams of 4–5 mm length. Categorization of substratum type was determined visually as silt-mud, sand-gravel, or cobble. The mean density of *Corbicula fluminea*, determined for each of the three substratum types by dividing number of individuals for each substratum type by number of square meter samples taken, was found to be highest in the sand/gravel substratum (7.5 individuals/m²). Cobble substrata yielded a mean number of 1.75 individuals/m². Silt/mud substrata had no clams. Sizes ranged from 6 to 27 mm although most clams sampled were in the 6–13 mm size category (87% of gravel-collected clams and 86% of cob-

ble-collected clams). The only substratum to contain all three size categories was gravel. Curiously, no clams of a size less than 6 mm were found in the cobble substratum. Mean size of all clams sampled was 8.81 mm ($n = 30$).

Distribution within Pueblo Reservoir was found to be relatively patchy. Although all areas sampled containing gravel or cobble yielded some clams, the density varied considerably. One sample area in particular yielded 51% of all the clams sampled for the entire survey. Density in this area was 19.0/m².

The presence of all size classes in Pueblo Reservoir, up to the largest clam, 27 mm, is indicative of a healthy population with immature individuals, recently mature adults, and reproductively active adults. A lack of small clams (less than 6 mm) in the cobble substratum may reflect both limitations in sampling methodology, as many small (< 4 mm) individuals were easily overlooked, as well as the difficulties associated with living in cobble substrata due to shell crushing by the cobbles or an inability to burrow among them. Patchiness could result from the lack of a planktonic larval stage. Larvae of *Corbicula fluminea* are brooded within the gills resulting in a fully formed juvenile released through the exhalant siphon in the immediate vicinity of the adult (McMahon, 1983). This causes a patch of clams to form after colonization around the original colonizers in an area.

The evidence presented here indicates that *Corbicula fluminea* may be propagating offspring in Pueblo Reservoir despite seasonal fluctuations in temperature and winter ice cover. The presence of the clams below the dam of John Martin Reservoir indicates that *C. fluminea* may be surviving in the deeper waters of the Arkansas River. The area receives river water from John Martin Reservoir through an opening at the base of the dam. This area is also very close to the bottom of the reservoir where colder bottom water flows under the dam.

All of these areas (Queen's Reservoir, John Martin Reservoir, and Pueblo Reservoir) are part of the Arkansas River drainage. Prior to these observations, *Corbicula fluminea* had never been documented in the Arkansas River in Colorado. A possible pathway for the spread of the species may be along the Arkansas River drainage. Populations in Arapahoe, Kiowa, and Bent Counties follow the drainage from the southwest. The population in Highline Lake, west of the Continental Divide, could be an introduction from the pet trade. At least one Denver area commercial pet dealer was selling *Corbicula* as an aquarium novelty (personal observation, August 1996). The University of Colorado Museum also includes one specimen (UCM 41599) purchased in 1992 from a Denver area mail order pet dealer. The Cherry Creek population may be indicative of dispersal down the South Platte drainage through Nebraska or another introduction. Cherry Creek Reservoir experiences a great deal of boat and

jet-ski traffic as well as recreational fishing whereby clams could be transported.

This species has clearly developed a foothold in two different Colorado drainages, the South Platte and Arkansas. Unfortunately, lack of mortality data prevents true measurements of cold tolerance. The presence of *Corbicula fluminea* in Colorado, especially in Pueblo Reservoir at an elevation of 5548 feet and temperatures often below freezing, and Highline Lake in Mesa County at an elevation of 4700 feet, is indicative of a rapid spread throughout the rest of the state in the near future.

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Cytotaxonomic Verification of a Non-Indigenous Marine Mussel in the Gulf of Mexico

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In 1990, invasive populations of the genus *Perna* of unknown origin(s) were reported from both the Caribbean and Gulf of Mexico; the mussel discovered in the Gulf of Mexico was identified as *P. perna* (Linnaeus, 1758) (Hicks & Tunnell, 1993), and that from the Caribbean as *P. viridis* (Linnaeus, 1758) (Agard et al., 1993). Although the identification of *P. viridis* in the Caribbean has been confirmed by protein electrophoresis (Agard et al., 1993), until now identification of *P. perna* in the Gulf was based

solely on morphology. It has been suggested that the Gulf mussel may be a brown morph of *P. viridis*, and that the two introductions were related.

It is difficult to reliably distinguish between *P. perna* and *P. viridis* due to their morphological similarity and considerable variation in taxonomically important morphological characters (Siddall, 1980; Sadacharan, 1982). With the possible exception of their sympatric occurrence in Sri Lanka and southern India, the mutually exclusive geographic distribution of *P. perna* and *P. viridis* has historically been of taxonomic value (Siddall, 1980; Agard et al., 1993). In situations where the geographic origin is unknown, as is usually the case with biological introductions, the high degree of phenotypic plasticity within this genus becomes more problematic, and alternative means of identification, such as cytogenetic techniques, are required (Beaumont et al., 1992; Insua et al., 1994).

In order to confirm the initial identification of the species in the Gulf of Mexico as *P. perna*, other, non-morphological characters were required. Cytological characters were selected based on their unambiguous nature and the known karyotypic dimorphism of the two taxa in question. *P. viridis* has 30 chromosomes and *P. perna*, 28 (Ahmed, 1974; Jacobi et al., 1990). In this paper we report the karyotype of the non-indigenous mytilid in the Gulf of Mexico for the first time, verifying its identity as *Perna perna*.

Materials and Methods

Specimens were collected from the north jetty at Mansfield Pass (26°34'N, 97°17'W), Padre Island National Seashore, Texas. Mussels were transported alive to the laboratory, then maintained in aerated tanks of seawater. Chromosome preparations were obtained from gill tissue using a modified colchicine-air drying Giemsa technique (Yaseen, 1996).

Mussels were incubated in aerated seawater in the presence of 0.05% colchicine at room temperature for 9 hours and the gill tissues dissected and placed in distilled water at room temperature for 30 minutes. Distilled water was replaced with a 0.8% sodium citrate hypotonic solution for 30 minutes. Tissues were then submerged in 50 mL tubes of fresh fixative (3 parts methanol:1 part acetic acid), changed two times for 20 minutes each, and then left in the fixative for 8 hours.

About 25 mg of gill tissue were then minced and disaggregated in a 70% glacial acetic acid solution to prepare a cell suspension. Disaggregated tissues were transferred via pipette back into fresh fixative, from which single drops of the cell suspension were allowed to fall onto glass slides placed at an angle of about 45°, from a height of 15 cm. Cell suspensions on slides were thoroughly air dried and stained with 5% Giemsa (diluted in phosphate buffer, pH 6.8) for 5 minutes. Black and white

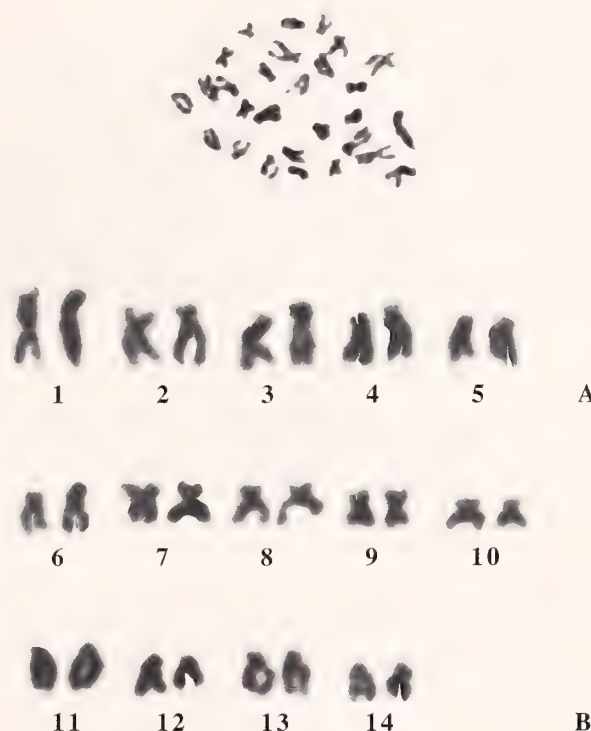


Figure 1

Micrograph of metaphase spread (top) and standard karyotype (bottom) of *Perna perna* ($2n = 28$) from the Gulf of Mexico. The 14 pairs of autosomes are diagnostic for *P. perna*, shown grouped by general morphology into two subsets of metacentric and submetacentric (A) and subtelocentric (B).

photomicrographs of well-spread mitotic metaphases were taken.

Results and Discussion

The diploid number of *P. perna* is 28 ($n = 14$), whereas that of *P. viridis* is 30 ($n = 15$) (Ahmed, 1974; Jacobi et al., 1990). A diploid number of $2n = 28$ was scored in twelve mitotic metaphases observed in six individuals of *Perna* from the northwestern Gulf of Mexico. Chromosomes were observed to vary from metacentric to subtelocentric, consistent with chromosome morphology presented by Jacobi et al. (1990) for *P. perna*. The standard karyotype of the Gulf of Mexico mussel consists of two groups based on overall chromosome morphology; one of 10 metacentric and submetacentric (A), and one of four subtelocentric chromosome pairs (B) (Figure 1). Groupings were based on qualitative observations. Thus, our observations confirm the original taxonomic identification and verify that the invader is *P. perna*. Furthermore, based on the largely allopatric natural distributions of *P. perna* and *P. viridis*, this result strongly suggests that there were two separate biological introductions involv-

ing mussels of the genus *Perna* in the Western Atlantic Ocean in 1990.

Acknowledgments

We would like to thank Marcos De Donato for technical assistance in the laboratory, and Yvette Barrios for assistance in the field. D. W. Hicks is supported by a grant from the Texas A&M Sea Grant College Program (NA56RG0388). Laboratory aspects of this study were supported by the TAMU Research Foundation.

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Rediscovery of the Introduced, Non-Indigenous Bivalve *Laternula marilina* (Reeve, 1860) (Laternulidae) in the Northeastern Pacific

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The non-indigenous *Laternula* (*Exolaternula*) *marilina* (Reeve, 1860) (Bivalvia: Laternulidae) has been rediscovered in the northeast Pacific in Humboldt Bay, California (40°49'N, 124°14'W). The first and only previous records of this species from the northeast Pacific are from Coos Bay, Oregon (43°25'N, 124°27'W) where two specimens were recovered from high intertidal mud flats in 1963, and a few specimens were recovered from marsh channels in 1966 (Keen, 1969). A photograph of these specimens, identified as *Laternula limicola*, is in the California Academy of Sciences (CAS) collections. However, the actual specimens cannot be found. No further records of *Laternula* from Coos Bay have been made since 1966 even though several systematic intertidal surveys of introduced species of Coos Bay were conducted between 1986 and 1997 (James T. Carlton, personal communication).

Laternula were collected from Humboldt Bay from salinities ranging between 28 and 34 psu at four out of 47 high intertidal stations sampled between June 1995 and December 1996 (Figure 1). Both live and empty shelled specimens were found. All live specimens but one (station 20, Figure 1) were recovered from northeast Humboldt Bay.

Laternula marilina may be commonly misidentified or overlooked in northeast Pacific bivalve collections due to its omission from major taxonomic references to eastern Pacific marine invertebrates and confusion with other species. Keen & Coan (1974) include *Laternula* in their key to marine molluscan genera of western North America. However, *Laternula* is not included in the bivalve keys of either of the general guides to invertebrates of the northeast Pacific (Smith & Carlton, 1975, and Kozloff, 1997), although it is cited (as *L. limicola*), but not illustrated, in the later reference. *Laternula limicola* (Reeve, 1863) of China is a synonym of *Laternula marilina* (Zhuang & Cai, 1982). This rediscovery of *Laternula* was too late for inclusion in the recent checklist of marine bivalves of the northeast Pacific, where it was excluded because it was thought to no longer be present (Coan & Scott, 1997).

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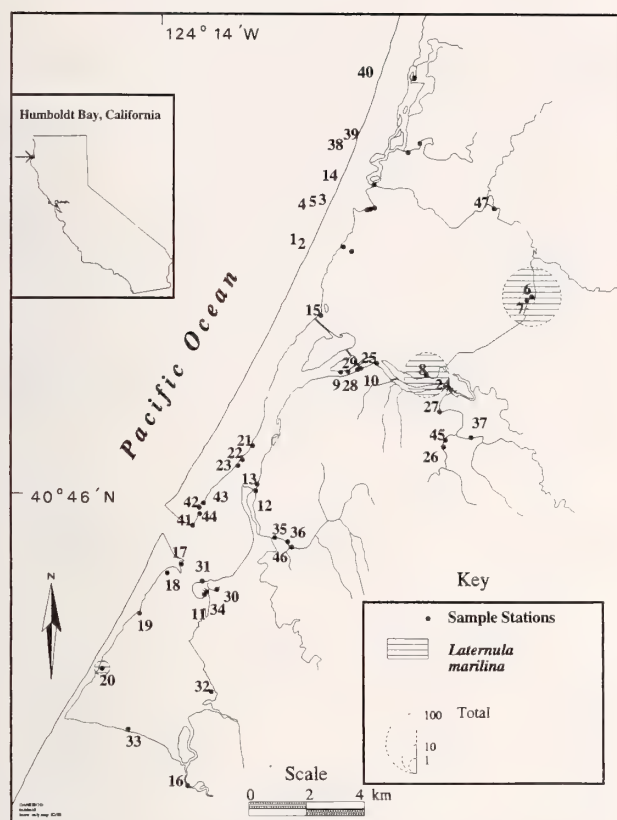


Figure 1

Humboldt Bay, California collection sites of the 1995–1996 intertidal benthic survey of macro-invertebrates with sites where *Laternula* were found indicated by crosshatched circles and scaled to the estimated population densities m^{-2} .

All presently known northeast Pacific *Laternula marilina* are small relative to Asian populations which attain lengths of 55 mm or more (Zhuang & Cai, 1982). The longest shell of any specimen from Humboldt Bay is 11.6 mm (Table 1), and the maximum length of the original specimens from Coos Bay is approximately 20 mm (Keen, 1969). The illustrations of Zhuang & Cai (1982) indicate a broader, more truncate posterior than occurs in the specimens from Humboldt Bay (Figure 2B). This variation appears to be entirely related to differences in size.

Laternula marilina has a chondrophore (Figure 2A) and a lithodesma on the ventral surface of its ligament. The external appearances of small individuals of this species resemble, and could be confused with, the common native clam *Cryptomya californica* (Conrad, 1837) and the introduced, non-indigenous clam *Mya arenaria* Linnaeus, 1758, which occur in similar habitats. *Laternula* s.s., lack a lithodesma. The presence of a lithodesma in *Laternula marilina* places it in the subgenus *Laternula* (*Exolaternula*).

Low densities and patchy local distributions of *Later-*

Table 1

Sample sites, numbers collected, estimated densities, and the averages and ranges of valve lengths, measured to ± 0.1 mm, of live *Laternula* (*Exolaternula*) *limicola* (Reeve, 1860) collected in the Humboldt Bay, California macro-invertebrate survey.

Sample site	Number	Density ^a (m^{-2})	Average length (mm)	Range of lengths (mm)
6	24	160.0	5.6	1.5–11.6
7	1	6.7	8.8	8.8
8	7	46.7	7.8	4.5–7.2
20	1	6.7	6.5	6.5

^a Density estimated from the remains of 10 4.4 cm diameter by 10 cm deep cores collected at each site and washed on a 0.5 mm mesh sieve.

nula populations in estuaries may account for the absence of recent records from Coos Bay and previous records from Humboldt Bay and other northeast Pacific estuaries, including San Francisco Bay. The largest previous macro-invertebrate survey of Humboldt Bay (Barnhart et al., 1992) included samples within channels and at the mouth of the bay, well away from where *Laternula* were recovered in this survey. The small sizes, extremely patchy distribution, and possible restriction of *Laternula* to high intertidal mud flats, where systematic surveys are seldom conducted, could make this species difficult to find even

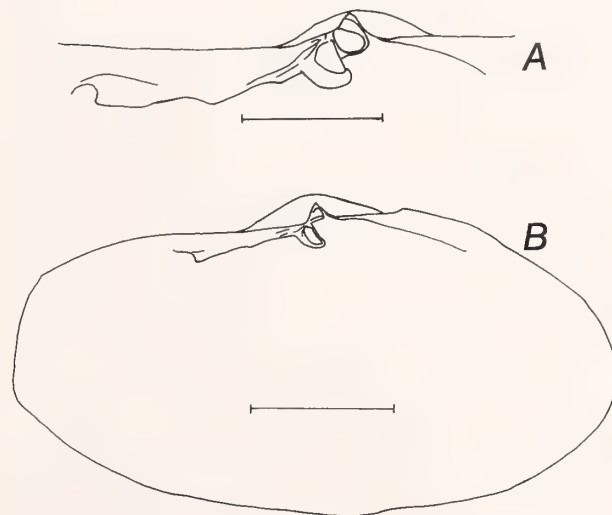


Figure 2

Hinge (A) and left valve (at slightly different angle) (B), with chondrophore, of an 8.5 mm length *Laternula* (*Exolaternula*) *limicola* (Reeve, 1860) from station 6, Humboldt Bay, California, California Academy of Sciences, Invertebrate Zoology, accession no. 50388, catalogue no. 111415.

in San Francisco Bay, where introduced species are relatively well known (Cohen & Carlton, 1995).

The variable northeast Pacific records of *Laternula* over time and among estuaries could also result from repeated local introductions and extinctions (species turnover). The small sizes of the northeast Pacific individuals relative to sizes reported from Asian populations may reflect relatively short life spans. Humboldt Bay and Coos Bay have numerous mechanisms for domestic introduction of *Laternula* from previously introduced but undiscovered northeast Pacific populations, including larvae carried in coastal currents, or in ballast water from commercial shipping (Carlton & Geller, 1995). Adult *Laternula* could also be transplanted to Humboldt Bay with domestic oyster transplants (Monroe et al., 1973; Barnhart et al., 1992) or with internationally transplanted Japanese oyster spat (Woelke, 1955) directly from its native range (central to northern Japan [Reeve, 1860] and China [Zhuang & Cai, 1982]). International ballast water traffic (Carlton & Geller, 1995) may also have carried the larvae to Humboldt Bay from Asia. These transport mechanisms could repeatedly carry in new populations which quickly decline to extinction in most areas and most instances. Such sporadic introductions would be difficult to detect. Resolution of these problems will require better definitions of the distribution and abundance of this species within and among the northeast Pacific estuaries over time.

Acknowledgments

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Chemoattraction of *Lymnaea elodes* (Gastropoda: Lymnaeidae) to Leaf Lettuce and Tetramin

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Introduction

Several studies have examined chemoattraction and dietary preferences of planorbid snails for Tetramin® (fish food) and leaf lettuce (Masterson & Fried, 1992; Marcopoulos & Fried, 1993; Mancina & Fried, 1995). However, studies using lymnaeid snails are not available. Sorensen et al. (1997) identified *Lymnaea elodes* (Say, 1821) (*L. elodes* = *L. palustris* = *Stagnicola palustris* = *S. elodes*) as a vector of the ubiquitous trematode *Echinostoma revolutum* (Froelich, 1802) in the USA. This species of lymnaeid is easy to maintain in the laboratory and achieves a length of 2 cm within 2 months. Because of its ease of maintenance, its relatively large size, and its role as a vector for an economically important trematode, it is a useful model for laboratory work.

This study examines chemoattraction of *L. elodes* to iceberg leaf lettuce (*Lactuca sativa*) and to Tetramin and

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Table 1

Chemoattraction of *Lymnaea elodes* snails to leaf lettuce and Tetramin.

Experiment	Choices	Percentage of snails in zones			Chi-square	P
		A	B	C		
1	Bl vs Bl	37	24	39	—	—
2	Bl vs L	29	17	54	9.54	0.008
3	Bl vs T	16	13	71	43.22	0.001
4	L vs T	24	15	61	20.35	0.016

Bl = blank; L = lettuce; T = Tetramin; each experiment was done 10 times; lettuce placed in zone C in Experiment 2 and zone A in Experiment 4; Tetramin placed in zone C in Experiments 3 and 4.

compares the results with our previous studies on planorbid snails.

Materials and Methods

Stock cultures of *Lymnaea elodes* were maintained in the laboratory on a diet of iceberg leaf lettuce occasionally supplemented with Tetramin (TetraWerke, Melle, Germany) as described by Frazer et al. (1997). The bioassay chamber for the study consisted of 100 × 15 mm petri dishes (Masterson & Fried, 1992). Two parallel lines were drawn 2.8 cm apart on the bottom of each petri dish to produce three zones (A, B, C). The side zones (A and C) each had an area of 14.1 cm², and the middle zone (B) had an area of 20.0 cm² (Masterson & Fried, 1992). Fifty-five mL of artificial spring water (ASW; Ulmer, 1970) was added to each dish. The snails were placed into the petri dish 10 min after the food or controls to allow adequate diffusion of food throughout the water. The dishes were maintained at 22 ± 1°C on a level work bench under overhead diffuse fluorescent light (Marcopoulos & Fried, 1993). Ten petri dishes were used for each trial.

Snails of approximately 20 mm shell length were maintained without food for approximately 3 hr prior to each trial. For each trial, a single snail was placed in the center of zone B in the bioassay chamber described above. Filter paper squares (1 cm²) were used as controls and placed at the edges of zones A and C. They were kept in place with paper clips. In the experimental trials, food items (also about 1 cm²) were used in place of the filter paper squares. Experimental trials matched lettuce versus blanks, Tetramin versus blanks, or lettuce versus Tetramin (see Table 1).

For 50 min, at intervals of 5 min, the zone in which the snail was located was recorded (a total of 10 observations per snail). A control group was used in each trial, as described above, to determine random movements of the snails. Random observations based on blank (control) experiments were used as the expected values to calculate

the chi-square value in each experimental design. A *P* value of less than 0.05 was considered significant (Mancia & Fried, 1995). Each experiment was done 10 times for every group.

Results and Discussion

The results of the chemoattraction trials are presented in Table 1. In trials that matched a food item against a control, snails were significantly attracted to either the lettuce or Tetramin (Experiments 2 and 3). In trials that matched lettuce against Tetramin (Experiment 4), snails were significantly attracted to the Tetramin.

Results of this study are in accord with the earlier findings on *Biomphalaria glabrata* (Say, 1818) (see Masterson & Fried, 1992) and *Helisoma trivolvis* (Say, 1816) (see Mancia & Fried, 1995) which showed significant chemoattraction to either lettuce or Tetramin in the presence of a blank control. The finding of significant chemoattraction of *Lymnaea elodes* to Tetramin rather than lettuce in our bioassay is in accord with that of Mancia & Fried (1995) on *H. trivolvis*, but differs from that of Masterson & Fried (1992) where *B. glabrata* showed no significant difference in chemoattraction between lettuce and Tetramin in the same bioassay. Unpublished observations by one of us (B.F.) suggest that growth and fecundity of *L. elodes* snails in the laboratory are suboptimal when maintained on Tetramin compared to those reared on leaf lettuce. Thus, snail chemoattraction to a food source is not an indicator that such a food item is optimal for growth and fecundity of that gastropod.

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**Lindeman Lake, British Columbia, Type Locality of
Zonitoides randolphi Pilsbry**

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Records of non-marine mollusks in western Canada are few but much repeated throughout the literature. Such is the case with Lindeman (or erroneously "Linderman") Lake, which is the northernmost locality (Bequaert & Miller, 1973) of *Discus shimekii* (Pilsbry, 1890) and the type locality of *Zonitoides randolphi* Pilsbry, 1898, a junior subjective synonym of *D. shimekii* according to Pilsbry (1948). Additionally, Lindeman Lake is cited elsewhere by Dall (1905), Baker (1911), Pilsbry (1948), and Clench & Turner (1962) in connection with this and other species of terrestrial and aquatic mollusks. A series of locality placements which were either imprecise or clearly wrong has most recently moved Lindeman Lake to the Yukon Territory (Bequaert & Miller, 1973).

The first appearance in the malacological literature of Lindeman Lake, as "Linderman Lake, Alaska," dates from the description of *Z. randolphi* by Pilsbry (1898); he may have assumed that the locality was in Alaska, or perhaps had been misinformed otherwise. The collector of the new species was P. B. Randolph of Seattle who published (1899) a brief popular account of his travels to the Klondike in 1897–1898. Randolph traveled north up the coast by ship and overland from Dyea, Alaska, via the Chilkoot Pass to the Yukon. Lindeman Lake was a stop en route on the Canadian side of the Chilkoot Pass; Randolph (1899:109) wrote:

We laid over one day at Lake Linderman [sic], resting from the past week's hard work, and I had time to hunt over the flat at the head of the lake where a small stream empties in.

Z. randolphi was among the species of terrestrial mollusks collected at Lindeman. However, nowhere in Randolph's account is the location of the lake ever stated.

Dall (1905:43) was the first to publish a correction to the earlier errors of Pilsbry and gave the locality as "Lake Lindeman, headwaters of the Yukon, British America." Most subsequent authors, including Pilsbry (1948), followed Dall who was essentially correct. (Canada was "British America" at that time.) However, more recently Bequaert & Miller (1973:57) placed Lindeman Lake in the Yukon Territory, "at the head of the Yukon River, ca. 64°30'N, 140°50'W," perhaps not realizing that the headwaters of the river system are in northwest British Columbia. The coordinates given by Bequaert & Miller are clearly erroneous.

Thus, the type locality of *Z. randolphi* and all other references to the locality should be corrected to read Lindeman Lake, British Columbia, Canada. The terminus of the Chilkoot Trail at the south end of Lindeman Lake is at ca. 59°47'N, 135°05'W (Energy, Mines and Resources

Canada, 1984). The small stream mentioned by Randolph (1899) could either be one of the branches of Lindeman Creek or a smaller, unnamed creek to the east.

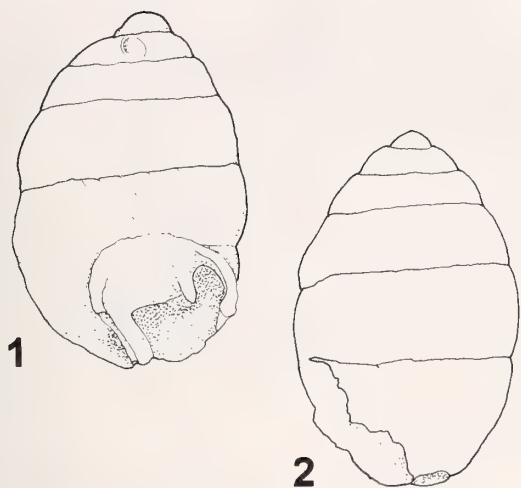
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**A New Species of *Gastrocopta*
(Gastropoda: Pulmonata: Pupillidae) from the
Deep River Formation, Late Oligocene or Early
Miocene, Montana**

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Roth & Emberton (1994) described an assemblage of land snail fossils from the Deep River Formation, continental deposits ranging from early Oligocene (Chadronian) to middle Miocene (Barstovian) age (Rensberger, 1981; Runkel, 1986), exposed in isolated outcrops in the Smith River Basin between White Sulphur Springs and Fort Logan, Meagher County, Montana. Based on the climatic signatures of extant genera, Roth & Emberton (1994) inferred a mesic climate with at least 75 cm/yr precipitation. In that paper, the present species was identified as *Gastrocopta* sp., aff. *G. armifera* (Say, 1821). Additional study of the material permits its description here as a new species.



Figures 1 and 2

Gastrocopta abyssifluminis Roth, sp. nov. Holotype, SBMNH 110599. Apertural and lateral views. Height 3.57 mm.

PUPILLIDAE Turton, 1831

Gastrocopta Wollaston, 1878

Type-species: *Pupa acarus* Benson, 1856; subsequent designation by Pilsbry (1916).

Gastrocopta abyssifluminis Roth, sp. nov.

(Figures 1, 2)

Gastrocopta sp., aff. *G. armifera* (Say), Roth & Emberton, 1994: 94.

Diagnosis: A large, broadly ovate *Gastrocopta* with 5.8–6.0 flattened whorls; suture appressed; base umbilicate, produced and compressed; inner end of angulo-parietal lamella curving toward periphery.

Description: Shell broadly ovate, widest above middle of body whorl; apical angle approximately 90°; base narrowly umbilicate, somewhat produced, tapering and compressed. Whorls 5.8 to 6.0 at maturity, with inconspicuous, raised, retractive growth lines; early whorls moderately convex; later whorls more flattened; suture appressed. Body whorl not strongly constricted behind aperture; crest absent. Aperture roughly triangular, acute at anterior end; parietal callus effuse, extending well onto face of body whorl. Strong angulo-parietal lamella present, inner end curving toward periphery; palatal and columellar lamellae not detected.

Dimensions: Holotype, height 3.57 mm; diameter 2.24 mm; height of body whorl 2.01 mm; whorls 6.75. Paratypes, height 3.15–3.99 mm (mean 3.63; $n = 11$); diameter 1.90–2.51 mm (mean 2.35; $n = 12$); height:diameter

ratio 1.34–1.80 (mean 1.55; $n = 11$); whorls 5.8–6.0 (mean 5.94, $n = 8$).

Type material: Holotype, Santa Barbara Museum of Natural History, SBMNH 110599, MONTANA: Meagher County: approximately 19 km northwest of White Sulphur Springs, 0.4–0.8 km east of White Sulphur Springs-Fort Logan road, in steep, bare north wall of small, meandering gully tributary to Rabbit Creek; sec. 14, T. 10 N, R. 5 E, Hanson Reservoir Quadrangle (USGS 7.5 Minute Series, Topographic, ed. 1971). Deep River Formation, late Oligocene or early Miocene. S. Stillman Berry et al. coll. 24 August 1941.

Paratypes (all from same locality as holotype): SBMNH 110298 (2 specimens), A. C. Silberling coll. 21 October 1940. SBMNH 110299 (10 specimens), A. C. Silberling coll. 21 October 1940, and S. Stillman Berry et al. coll. 24 August 1941; SBMNH 111989 (2 specimens), collector not stated, 28 August 1954.

Referred material: In addition to the type material, 15 specimens from the Berry collection are not designated as types because they are poorly preserved or imperfectly labeled as to locality.

Remarks: The type locality of *Gastrocopta abyssifluminis* is the same as that of *Euchemotrema occidentale* Roth & Emberton, 1994, and *Hendersonia stillmani* Roth & Emberton, 1994, and probably equivalent to the Spring Creek 1 locality of Rensberger (1981). The presence of *Pupoides montana* Pierce, 1992, in the molluscan assemblage from this locality (Roth & Emberton, 1994) suggests correlation with the Cabbage Patch Beds in western Montana (Pierce & Rasmussen, 1992), of Arikareean age. *Gastrocopta abyssifluminis* is not among the Pupillidae reported from the Cabbage Patch Beds: it is substantially larger than *G. obesa*, *G. oviforma*, *G. tavennerensis*, *G. leonardi*, and *G. minuscula* (all, Pierce in Pierce & Rasmussen, 1992) and has less impressed sutures than any of them. It is relatively broader than *G. russelli* Pierce, 1992 (height:diameter ratio 1.34–1.80 compared to 1.64–1.92 for *G. russelli*), with more tapering anterior end and flatter whorls; the inner end of the angulo-parietal lamella curves toward the periphery rather than toward the columella.

Etymology: L., *abyssus* (deep, bottomless) + *flumen, fluminis* (stream): of the Deep River Formation.

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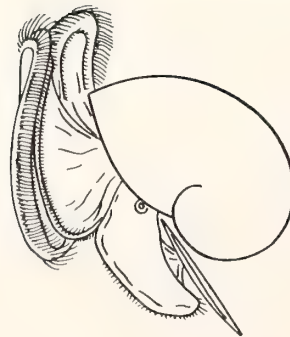
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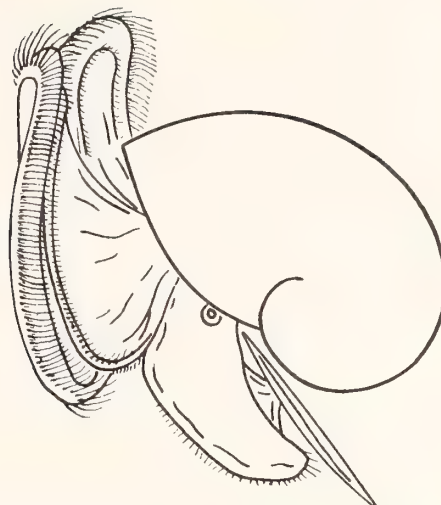
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Another Look at the Muricine Genus *Attiliosa*

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This paper is fondly dedicated to the memory of the late Anthony D'Attilio.

Abstract. Prior to this study, the muricine genus *Attiliosa* comprised 13 (or possibly 14) species, known from tropical waters around the world, and ranging in age from Oligocene to Recent. Of this number, four were known from the fossil record: two (or three) from Europe, and two from the New World. The present study adds seven new species. Of these, three are fossil forms: *A. gretae*, from the Early Miocene Chipola Formation, northwestern Florida; *A. macgintyi*, from the Pliocene Tamiami Formation, southern Florida; and *A. gibsonsmithi*, from the Late Miocene Mataruca Member, Caujaro Formation, Venezuela. The four Recent species are: *A. bessei* and *A. kevani*, from the Caribbean; *A. perplexa*, from Brazil; and *A. houarti*, from the eastern Indian Ocean (Thailand).

INTRODUCTION

Seventeen years ago a review of the genus *Attiliosa* Emerson, 1968, noted that it "is a small muricine group with but a few species" (Vokes & D'Attilio, 1982:67). In that review, we recognized a total of five or six living species. There was a single eastern Pacific species [*A. nodulosa* (Adams, 1855)], and two western Atlantic ones [*A. aldridgei* (Nowell-Usticke, 1969) and *A. philippiana* (Dall, 1889)]. In the Indo-Pacific area there were two [*A. nodulifera* (Sowerby, 1841) and *A. orri* (Cernohorsky, 1976)], and possibly a third [*A. caledonica* (Jousseume, 1881)], which might or might not be a synonym of *A. nodulifera*. However, additional material has shown *A. caledonica* to be a valid species.

At that time, the fossil record in the New World consisted of a few specimens of *A. aldridgei* from the Mio-Pliocene Gurabo Formation, Dominican Republic, and a single example of *A. nodulosa* from the Early Pliocene Esmeraldas beds, Onzole Formation, of northwestern Ecuador.

However, the group also has a long history in the Old World where there is an apparently unnamed species in the Oligocene Stampian of France that is markedly similar to *A. attiliosa* (compare Figure 1 and Figure 17, for example). There is a second French species of Middle Miocene Burdigalian age, originally named *Taurasia sacyi* by Cossmann & Peyrot (1923:257, pl. 13, figs. 31, 32) that may or may not be a synonym of the contemporaneous Italian *Fusus villae* Michelotti, 1847. The original illustration of the latter (Michelotti, 1847:pl. 10, fig. 11) is poor, but it was somewhat better illustrated by Belardi (1872:pl. 9, fig. 20). On the basis of these illustrations, it is probable that *A. villae* and *A. sacyi* are the same species, but with no Italian material available for study, this is not certain.

Thus, in 1982, there was a total of seven (or nine) known species of *Attiliosa*: two (or maybe three) occurring in the fossil record of Europe: three in the Recent fauna of the New World (two of these also occurring in the fossil record) and possibly three Recent Indo-Pacific forms. Since that time, there have been five additional living species described: *A. goreensis* Houart, 1993, from the eastern Atlantic (Senegal); *A. glenduffyi* Petuch, 1993, from the western Atlantic; *A. bozzettii* Houart, 1993, from the western Indian Ocean (Somalia); *A. ruthae* Houart, 1996, from the Philippine Islands; and *A. edingeri* Houart, 1998, from Western Australia.

In the last 17 years much new material has been made available, both fossil and Recent. This paper adds three new fossil species from the western Atlantic, and four new Recent species, three from the western Atlantic and one from the Indian Ocean. Synonymies for those Recent species covered previously (Vokes & D'Attilio, 1982) are not complete but include only the original references and those citations subsequent to 1982; the reader is referred to that paper for more complete information. Likewise, the European fossil species are not treated systematically due to lack of information.

On the basis of morphological similarities, there is one group of species beginning with the French Oligocene *Attiliosa* sp. (Figure 1) and including the modern *A. aldridgei*, *A. bessei*, and *A. kevani*, in the western Atlantic. The eastern Atlantic *A. goreensis* is extremely similar to the Oligocene *Attiliosa* sp. and also may be included as a member of the "*aldridgei* complex." The more squamose Indo-Pacific *A. bozzettii* and *A. houarti* and the spinose *A. orri*, although less similar in morphology are, nevertheless, close enough to indicate that they too should be placed in this group, as are *A. nodulifera*, *A. caledonica*, and *A. ruthae*. All of these species share a rounded aperture, with an expanded columellar lip and a surface

ornamentation that is more or less scabrous, sometimes with small spines developed at the intersection of the spiral and axial ornamentation.

A second morphological grouping would include: the French Miocene *A. sacyi* (Figure 2); the two new western Atlantic fossil species *A. macgintyi* and *A. gibsonsmithi*; *A. nodulosa* in the eastern Pacific; *A. philippiana* in the Caribbean; and perhaps *A. perplexa* on the coast of Brazil. These species share an elongated aperture with a narrow columellar lip and, with the exception of *A. perplexa*, no varical spines. The recently described Australian species *A. edingeri* bears a sufficient resemblance to the eastern Pacific *A. nodulosa* to be included also in this group. A third more distantly related set begins with the Early Miocene *A. gretae* in northwestern Florida, and includes only the living Caribbean *A. glenduffyi*.

ABBREVIATIONS FOR REPOSITORIES OF FIGURED SPECIMENS

AMNH, American Museum of Natural History, New York, New York, USA; IRSNB, Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; MNHN, Muséum National d'Histoire Naturelle, Paris, France; NMB, Naturhistorisches Museum, Basel, Switzerland; SDSNH, San Diego Natural History Museum, San Diego, California, USA; UF, Florida Museum of Natural History, University of Florida, Gainesville, Florida, USA; USNM, National Museum of Natural History, Washington, DC, USA.

SYSTEMATICS

Family MURICIDAE Rafinesque, 1815

Subfamily MURICINAE Rafinesque, 1815

Genus *Attiliosa* Emerson, 1968

Attiliosa Emerson, 1968:380.

Type species: *Coralliophila incompta* Berry, 1960 (= *Peristernia nodulosa* A. Adams, 1855), by original designation.

Diagnosis: Shell stoutly biconic; axial ornamentation of six to 12 rounded ridges, rarely with short spinose processes developed at intersection of axial and spiral ornamentation; aperture large, with nodules or lirations on inner side of outer lip and two or three nodules at anterior end of columellar lip; siphonal canal short, recurved, forming siphonal fasciole.

Discussion: The relatively small (both in number of species and size of shell) genus *Attiliosa* is what one might consider the "tag-end" of the subfamily Muricinae. These plain shells bear little familial resemblance to the more elaborately varicose groups in the subfamily, such as *Murex* or *Chicoreus*. In most cases, the shells are almost non-varicate, with little more than axial ridges to mark previous positions of the aperture. On some species there are short spinose processes on the varices, e.g., *A. nodulifera* (Figure 43), which led to its original definition in the genus *Murex*, but the majority bear no more than a few spinelets, if any.

This non-varicate morphology has led to a great deal of confusion among workers as to the systematic position of the few species named prior to Emerson's recognition (1968:370) of the true nature of the genus, with its muricine radula. As a measure of the dubious appearance of the members of this genus, they have been placed at various times in the following genera: *Coralliophila*, *Calotrophon*, *Drupa*, *Fusus*, *Latiaxis*, *Murex*, *Muricopsis*, *Muricidea*, *Ocenebra*, *Peristernia*, *Phyllonotus*, *Poirieria*, *Ocenebra*, *Taurasia*, *Trophon*, *Typhis*, *Vasum*, and probably others!

The shells that have engendered this confusion may be characterized as stoutly biconic and generally small for the subfamily (most specimens are under 30 mm in length). There are from six to 12 axial ridges, which may or may not have small spinose processes, and the shell surface varies from scabrose to smooth. The aperture is relatively large, varying from round to elongate, and an anal channel may be present. The most distinctive generic characters are the strong elongate nodules or lirations on the inner side of the outer lip that may extend well back

→

Explanation of Figures 1 to 9

Figure 1a, b. *Attiliosa* sp. USNM 377398; height 17.7 mm, diameter 10.4 mm; locality: Gaas, France, Stampian. ×3.

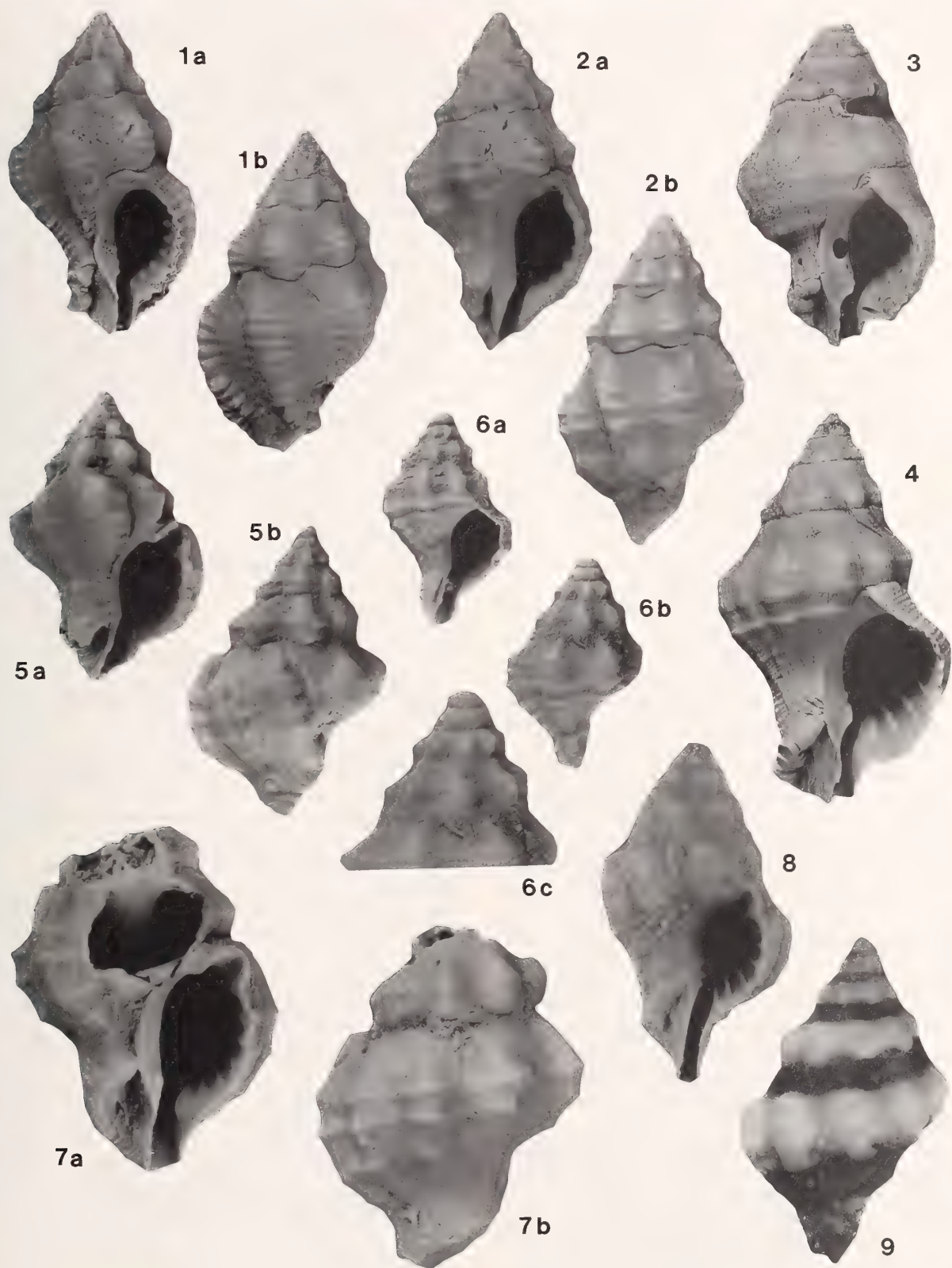
Figure 2a, b. *Attiliosa sacyi* (Cossmann & Peyrot, 1923). NMB H-18088; height 13.2 mm, diameter 7.4 mm; locality: St. Paul, Dax, France, Burdigalian. ×4.

Figures 3 and 4. *Attiliosa nodulosa* (A. Adams, 1855). Figure 3. USNM 418059; height 25.7 mm, diameter 16.6 mm; locality: TU 1399, Esmeraldas beds, Onzole Formation. ×2. Figure 4. USNM 859927; height 31.5 mm, diameter 19.0 mm; locality: TU R-487, Guaymas, Sonora, Mexico. ×2.

Figures 5–7. *Attiliosa gretae* E. H. Vokes, sp. nov. Figure 5a, b.

USNM 498197 (Holotype); height 7.7 mm, diameter 4.9 mm; locality: TU 458, Chipola Formation ×6. Figure 6a, b. USNM 498198 (Paratype A); height 5.7 mm, diameter 3.7 mm; locality: TU 819, Chipola Formation. Figure 6a, b ×6; 6c ×10. Figure 7a, b. USNM 498199 (Paratype B); height 9.3 mm, diameter 7.2 mm; locality: TU 819, Chipola Formation. ×6.

Figures 8 and 9. *Attiliosa glenduffyi* Petuch, 1993. Figure 8. USNM 860299; height 13.9 mm, diameter 8.0 mm; locality: Dominican Republic. ×4. Figure 9. USNM 860298; height 14.3 mm, diameter 9.2 mm; locality: Dominican Republic (shell not whitened, to show color pattern). ×4.



into the aperture, and the two or three elongate nodules (reduced to only one in *A. perplexa*) on the anterior portion of the columellar lip, which may or may not be expanded at the anterior end. The siphonal canal is short and recurved distally, which gives rise to a siphonal fasciole.

From the list of "possible" genera cited above, the members of the genus *Attiliosa* may be separated from most by the presence of a muricine radula and operculum. *Murex* and *Phyllonotus* were used only in the broadest sense and, as defined today, have little resemblance. *Calotrophon* and *Poireria* (*Panamurex*) are the two most similar appearing taxa; the morphological similarity is close to some species, especially the Miocene *Calotrophon phagon* (Gardner, 1947) and *Poireria* (*Panamurex*) *mauryae* Vokes, 1970. Both of these species share with *Attiliosa* the columellar nodules and labral lirations, causing us previously (Vokes & D'Attilio, 1982:68) to suggest that *Attiliosa* originated as a branch of the *Poireria* clan. Discovery of the Oligocene species assigned to *Attiliosa* pushes the separation further back in time; nevertheless it is to the *Poireria* clan that *Attiliosa* bears the strongest morphological similarity.

In the Muricidae, convergence of shell form is a common problem. Thus, one branch of *Panamurex*, beginning with *P. mauryae*, in time has moved in the direction of shell simplification, resulting in the Recent *P. (P.) velero* Vokes, 1970, which becomes morphologically much like *Attiliosa*, differing primarily in the strong spiral ornamentation, more inflated whorls, and more elongate overall outline. However, *Calotrophon*, in time, has gone in the direction of greater shell ornamentation, as well as losing the columellar nodules, so that the living members of *Calotrophon* are less easily confused with *Attiliosa*.

In the final analysis, one must be reminded once again that the concept of generic separation is completely artificial and is "in the eye of the beholder." We are attempting to separate the colors of the spectrum into discrete boxes. Which box one places which species in is largely subjective. There are certain forms that are unequivocal (like red, yellow, or blue) but others are less certain (does turquoise belong with blue or green?).

Those species that are here grouped in the concept called *Attiliosa* share a short "squatty" shell outline, with usually a rounded shoulder. Most are non-varicate. But none of these attributes is absolute: *A. macgintyi* has a distinctly diamond-shaped outline, and both *A. nodulifera* and *A. orri* have spinose varices. The alternative to accepting these exceptions is to create yet more smaller boxes to contain them, and in time this may well happen, if enough additional similar appearing forms are discovered. After all, we started with one genus *Murex*, which has been repeatedly subdivided into first more genera, then into families and subfamilies.

The solution, at this time, is to divide the genus into "species-complexes," which at some future date might

well become recognized genus-group taxa. On the basis of shell morphology, the genus *Attiliosa* may be separated into three distinct species-complexes, as follows:

- (1) The *aldridgei*-complex, characterized by a rounded aperture, expanded columellar lip, more or less scabrous surface ornamentation, sometimes with small spines developed at the intersection of the spiral and axial ornamentation. This complex includes: the unnamed French Oligocene species; *A. aldridgei*, *A. bessei*, *A. kevani*, in the western Atlantic, and *A. goreensis*, in the eastern Atlantic; *A. bozzettii*, *A. orri*, *A. houarti*, in the Indian Ocean; and *A. nodulifera*, *A. caledonica*, and *A. ruthae* in the Pacific.
- (2) The *nodulosa*-complex, characterized by an elongated aperture, narrow columellar lip, more or less smooth surface ornamentation, and no varical spines (with the exception of *A. perplexa*). This complex includes: *A. sacyi* (?+*A. villae*), from the Miocene of Europe; *A. gibsonsmithi*, *A. macgintyi*, *A. philippi-ana*, and *A. perplexa*, in the western Atlantic; *A. nodulosa* in the eastern Pacific; and *A. edingeri* in the Indian Ocean.
- (3) The *glenduffyi*-complex, distinguished from the others by a marked anal channel and including only the Miocene *A. gretae* and the Recent western Atlantic *A. glenduffyi*.

FOSSIL SPECIES

Attiliosa gretae E. H. Vokes, sp. nov.

(Figures 5–7)

Description: Shell small for the genus (maximum height approximately 12 mm); protoconch of two large, smooth bulbous whorls, ending at small varix. Axial ornamentation on all teleoconch whorls of eight rounded ridges; on earliest teleoconch whorls small open flanges on abapertural side of ridges but these disappearing by about fourth teleoconch whorl. Spiral ornamentation of one strong cord at shoulder, on early whorls several smaller cords anterior to shoulder but most weakening as shell increases in size, leaving just two cords anterior to shoulder; one smaller cord on siphonal canal. Where spiral cords cross axial ridges weak pointed knobs developed; otherwise, shell surface smooth. Suture appressed, sinuated by axial ridges. Aperture oval, marked anal channel; columellar lip smooth except for two small denticles at anterior end; inner side of outer lip with seven strong lirae extending well into aperture. Siphonal canal short, broad: siphonal fasciole increasing in width with increasing shell size. Traces of heavy intritacalx indicating that in life shell surface was covered by this chalky layer.

Holotype: USNM 498197; height 7.7 mm, diameter 4.9 mm (Figure 5).

Type locality: Chipola Formation; TU 458, east bank of

Chipola River, above Farley Creek (SW $\frac{1}{4}$ sec. 20, T. 1 N, R. 9 W), Calhoun County, Florida.

Paratype A: USNM 498198; height 5.7 mm, diameter 3.7 mm; locality: TU 819 (Figure 6).

Paratype B: USNM 498199; height 9.3 mm, diameter 7.2 mm; locality: TU 819 (Figure 7).

Occurrence: Chipola Formation, TU localities 458, 547, 548, 817, 819, 999, 1196.

Discussion: For some time, we have had a dozen specimens of a small species taken from primarily coralline localities in the Chipola Formation, northwestern Florida. Obviously muricid, the exact generic placement was a puzzle until the discovery of *A. glenduffyi*, living off the shores of the Dominican Republic. This Recent form shares with the Chipola shell a marked anal channel and axial ornamentation consisting of rounded ribs but no true varices. However, *A. gretae* differs from *A. glenduffyi* in having a lower spire, a shorter siphonal canal, and a less appressed suture. Both species are small, although the Chipola form is slightly smaller, with a maximum size of 12 mm, but *A. glenduffyi* attains an adult size of approximately 15 mm. Although difficult to see in the photograph, paratype B shows typical *Attiliosa* nodules at the base of the columellar lip.

In addition to the Tulane material, there are four specimens in the private collection of Mr. and Mrs. Andrew Murray, of Bradenton, Florida. It is a pleasure to name this new species in honor of Greta (Mrs. Andrew) Murray, for her excellent work on the Chipola fauna, including collecting paratype B.

Attiliosa gibsonsmithi E. H. Vokes, sp. nov.

(Figures 10–13)

Description: Shell large for the genus (maximum height approximately 25 mm), inflated in outline. Protoconch of one and three-quarters smooth, bulbous whorls; six teleoconch whorls. Axial ornamentation of nine or 10 swollen axial ridges on each whorl. Spiral ornamentation very faint on early whorls, gradually increasing in strength and becoming three flattened cords on spire whorls; approximately six spiral cords on body whorl, that at base of body whorl the largest. Suture appressed, sinuated by axial ridges. Aperture round; inner lip smooth, appressed entire length; two weak nodules at anterior end. Margin of outer lip crenulated by spiral cords, a small projection formed by cord at base of body whorl; nine thin lirae extending far back into aperture. Siphonal canal short, broad; recurved at distal end, forming deep siphonal fasciole.

Holotype: NMB H-18084; height 19.2 mm, diameter 12.8 mm (Figure 10).

Type locality: Mataruca Member, Caujaro Formation; NMB 17530, Cementerio de Carrizal, Falcón, Venezuela.

Paratype A: NMB H-18085; height 20.4 mm, diameter 11.9 mm (Figure 11).

Paratype B: NMB H-18086; height 20.0 mm, diameter 12.3 mm (Figure 12).

Paratype C: NMB H-18087; height 14.3 mm, diameter 8.3 mm (Figure 13). Locality of all same as holotype.

Occurrence: All material from type locality.

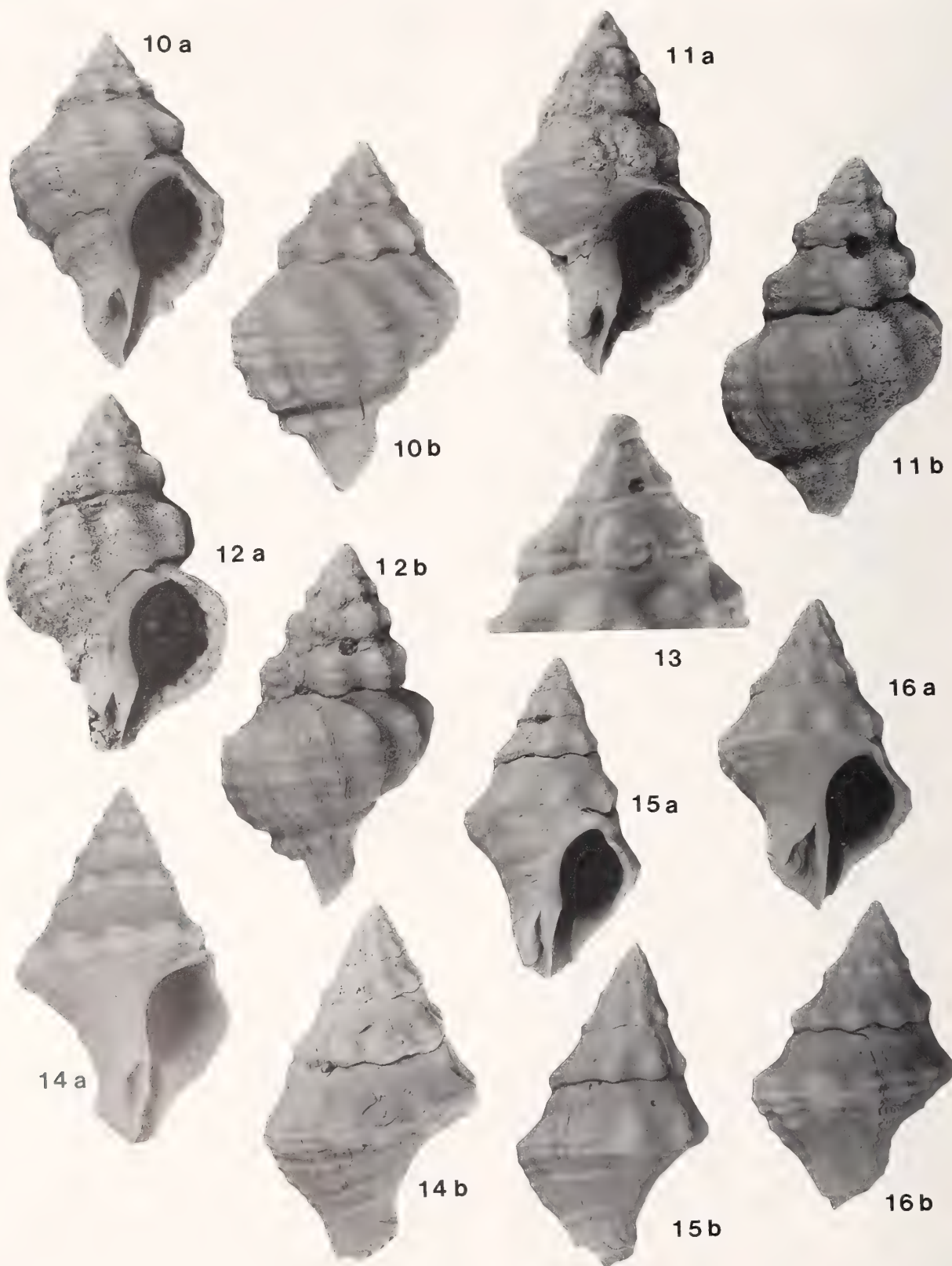
Discussion: In the collections of the Naturhistorisches Museum, Basel, Switzerland, there are 35 examples of a second new species, taken from Late Miocene aged beds of the Mataruca Member of the Caujaro Formation, Venezuela. This species also has been a puzzle for many years. The type material was originally sent to me by the collectors, Mr. and Mrs. Jack Gibson Smith, then of Caracas, Venezuela, now of Surrey, England. But neither they nor I could come up with any unequivocal generic placement for the form. With the recognition of Cossmann & Peyrot's *Taurasia sacyi* as a member of *Attiliosa*, similarity to the Venezuelan material indicated placement here might also be appropriate. Morphologically, they both have a strong basal cord, separated from the body whorl, which has rounded axial ribs but no true varices. The suture is sinuated by the axial ribs, and the aperture is strongly lirate within. But *A. sacyi* is much smaller and more evenly biconic in outline, *A. gibsonsmithi* having more inflated whorls.

In the living fauna the species most nearly akin to *A. gibsonsmithi* is that found off the west coast of tropical America, *A. nodulosa* (Adams), which differs from the older species in having a more appressed suture. So, possibly, *A. sacyi* gave rise to *A. gibsonsmithi*, which in turn gave rise to *A. nodulosa*, forming a species-complex long separate from the other Atlantic species. If *A. sacyi* also gave rise, independently, to the *A. philippiana* line, this would explain the similarity between the Pacific *A. nodulosa* and the Atlantic *A. philippiana*.

Attiliosa macgintyi E. H. Vokes, sp. nov.

(Figures 14–16)

Description: Shell biconic in outline; six teleoconch whorls in adult, early whorls unknown. Axial ornamentation of 11 or 12 rounded ridges on each teleoconch whorl. Spiral ornamentation of low raised cords, only two visible on spire whorls; approximately three on body whorl and three on siphonal canal, but number varying greatly between specimens. Where spiral cords cross axial ridges small nodes developed, otherwise shell surface smooth. Suture appressed, undulated by axial cords; shoulder very sloping. Aperture diamond-shaped, slight anal channel at posterior end. Columellar lip smooth, ap-



pressed posteriorly, free-standing anteriorly; two small nodules at anterior end. Inner side of outer lip with seven lirae extending well into aperture. Siphonal canal short, broad, recurved at distal end; deep siphonal fasciole.

Holotype: UF 90727; height 24.3 mm, diameter 14.7 mm (Figure 14).

Type locality: Tamiami Formation; UF CR007 (= TU 797), material exposed during construction of "Alligator Alley," 13.3 miles east of Florida Highway 29 (T. 49 S, R. 32 E) Collier County, Florida.

Paratype A: UF 90728; height 21.8 mm, diameter 12.8 mm (Figure 15).

Paratype B: UF 90729; height 20.9 mm, diameter 13.6 mm (Figure 16).

Locality: of both same as holotype.

Occurrence: All material from type locality.

Discussion: In the collection of the late Tom McGinty, Palm Beach, Florida, now located at the Florida Museum of Natural History, there are three examples of a new species originally taken from exposures of the Tamiami Formation available during construction of "Alligator Alley" (Florida Highway 84), southern Florida. Unfortunately, the three known specimens are badly worn, and details of early whorls are lacking. These shells bear some resemblance to the Recent *A. philippiana*, but differ in having a striking expansion at the periphery, a less appressed suture, and a somewhat larger size. The new species attains a maximum size of about 25 mm in contrast to a maximum of under 20 mm for *A. philippiana*. The overall outline of the shell is much closer to that of the Middle Miocene *A. sacyi*, suggesting that this new form is intermediate between the latter and *A. philippiana*.

Attiliosa aldridgei (Nowell-Usticke, 1969)

(Figures 17–25)

Vasum aldridgei Nowell-Usticke, 1969:18, pl. 4, fig. 834.

Attiliosa aldridgei (Nowell-Usticke). Nowell-Usticke, 1971:

11, pl. 2, fig. 680; Vokes & D'Attilio, 1982:69, figs. 6–9; Vokes, 1989:62, pl. 6, figs. 9, 10; Vokes, 1992:93, pl. 20, figs. 5–8; Houart, 1993a:21, fig. 14.

Holotype: American Museum of Natural History, no. AMNH 189620; height 29.4 mm, diameter 20.0 mm.

Type locality: Rat Island, Antigua, B.W.I.

Fossil occurrences: TU localities 283, 727 (Bermont Formation); 1215 (Gurabo Formation), 1422 (Cercado Formation); 1240 (Moín Formation).

Figured specimens:

Figure 17. AMNH 168901 (Paratype); height 22.4 mm, diameter 14.0 mm; locality: Antigua, B.W.I.

Figure 18. USNM 890890; height 29.7 mm, diameter 18.3 mm; locality: Bimini, B.W.I., 10 meters.

Figure 19. USNM 792393; height 12.3 mm, diameter 8.2 mm; locality: Bimini, B.W.I., 10 meters.

Figure 20. USNM 890891; height 16.4 mm, diameter 10.5 mm; locality: Discovery Bay, Jamaica, 10 meters.

Figure 21. USNM 869515; height 19.1 mm, diameter 12.8 mm; locality: TU R-369, Moín, Costa Rica.

Figure 22. USNM 498200; height 20.1 mm, diameter 11.7 mm; locality: TU 1422, Cercado Formation.

Figure 23. USNM 890892; height 20.7 mm, diameter 12.4 mm; locality: TU R-109, Bahía de Las Minas, Panama.

Figure 24. USNM 890893; height 15.1 mm, diameter 9.2 mm; locality: Cartagena, Colombia.

Figure 25. USNM 323924; height 10.8 mm, diameter 6.9 mm; locality: TU 1240, Moín Formation.

Discussion: For a complete synonymy of citations prior to 1982, see Vokes & D'Attilio (1982:69). At that time, the species was known from a relatively few individuals, collected from Bimini, B.W.I. to Panama. Since that original discussion we have obtained numerous additional Recent specimens from other Caribbean Recent localities, and several fossil examples, especially from the coral-reefs of the Cercado and Gurabo formations (Mio-Pliocene) of the Dominican Republic, as well as the Caloosahatchee and Bermont formations of Florida.

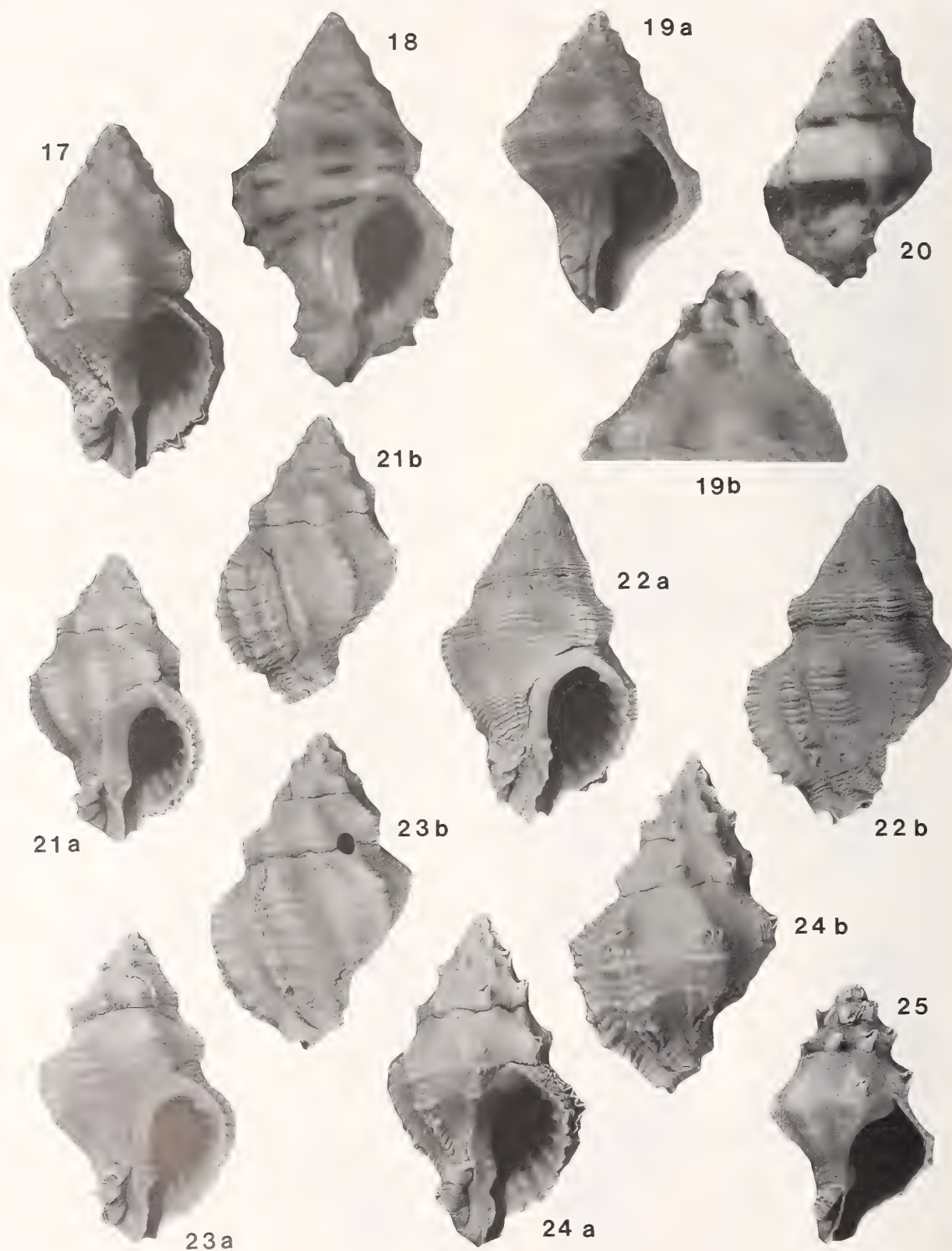
There is a fair degree of variability in the overall mor-

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Explanation of Figures 10 to 16

Figures 10–13. *Attiliosa gibsonsmithi* E. H. Vokes, sp. nov. Figure 10a, b. NMB H-18084 (Holotype); height 19.2 mm, diameter 12.8 mm; locality: NMB 17530, Mataruca Member, Caujaro Formation. ×3. Figure 11a, b. NMB H-18085 (Paratype A); height 20.4 mm, diameter 11.9 mm; locality: same as holotype. ×3. Figure 12a, b. NMB H-18086 (Paratype B); height 20.0 mm, diameter 12.3 mm; locality: same as holotype. ×3. Figure 13. NMB H-18087 (Paratype C); height 14.3 mm, diameter 8.3 mm; locality: same as holotype. ×10.

Figures 14–16. *Attiliosa macgintyi* E. H. Vokes, sp. nov. Figure 14a, b. UF 90727 (Holotype); height 24.3 mm, diameter 14.7 mm; locality: UF CR007 (= TU 797), Tamiami Formation. ×2.5. Figure 15a, b. UF 90728 (Paratype A); height 21.8 mm, diameter 12.8 mm; locality: same as holotype. ×2.5. Figure 16a, b. UF 90729 (Paratype B); height 20.9 mm, diameter 13.6 mm; locality: same as holotype. ×2.5.



phology of this species. Some specimens are low-spined and "chunky" (e.g., Figures 21 and 23), and some have a higher spire, with an impressed suture, which gives a "stepped" appearance to the shell (e.g., Vokes & D'Attilio, 1982:fig. 7). Although the two "chunky" examples figured here both come from the southern Caribbean, there does not seem to be any particular geographic distribution to the differences. In the Mio-Pliocene beds of the Dominican Republic, both forms occur together (compare Vokes, 1989:pl. 6, figs. 9, 10). The southern forms have a more lirate aperture and also are more spinose in the younger stages (compare Figure 19 with Figures 24, 25). Given the similarity of the adult specimens, there seems little reason to separate the southern form as a distinct species from the more northern typical examples, but rather to accept them as the end members of a single cline.

The typical form is ornamented by thin brown lines topping the spiral cords (Figure 18), but some specimens have a single broad color broad at the periphery (Figure 20). This latter color morph was named *Muricopsis poeyi* by Sarasúa & Espinosa (1979:2, fig. 1; holotype refigured by Vokes & D'Attilio, 1982:fig. 10). The only examples I have seen with such a pattern come from the Greater Antilles, and this may be a geographic variation.

Attilosa nodulosa (A. Adams, 1855)

(Figures 3, 4)

Peristernia nodulosa A. Adams, 1855:313.

Coralliophila incompta Berry, 1960:119.

Attilosa nodulosa (Adams). Vokes & D'Attilio, 1982:69; Vokes, 1988:33, pl. 6, figs. 5, 6.

Syntypes: The Natural History Museum, London [British Museum (Natural History)]; see Bullock, 1976:pl. 1, figs. 6, 8.

Type locality: "Australia."

Fossil occurrence: Esmeraldas beds, Onzole Formation, TU locality 1399.

Figured specimens:

Figure 3. USNM 418059; height 25.7 mm, diameter 16.6 mm; locality: TU 1399, Esmeraldas beds, Onzole Formation.

Figure 4. USNM 859927; height 31.5 mm, diameter 19.0 mm; locality: TU R-487, Guaymas, Sonora, Mexico.

Discussion: For a complete synonymy and discussion of the convoluted nomenclatorial history of this species, which is the type of the genus *Attiliosa*, see Vokes & D'Attilio (1982:69). Discovery of a fossil specimen in the Early Pliocene Esmeraldas beds, Onzole Formation, of northwestern Ecuador (Vokes, 1988:pl. 6, fig. 6; refigured here, Figure 3), reveals a considerable geologic history for the eastern Pacific species.

RECENT SPECIES

Attiliosa glenduffyi Petuch, 1993

(Figures 8, 9)

Attiliosa sp. Vokes, 1992:95, pl. 20, figs. 10, 11.

Attiliosa glenduffyi Petuch, 1993:54, figs. 6, 7.

Holotype: Carnegie Museum of Natural History; height 13 mm, diameter 9 mm (*vide* Petuch, 1993:54).

Type locality: Samana, Dominican Republic.

Figured specimens:

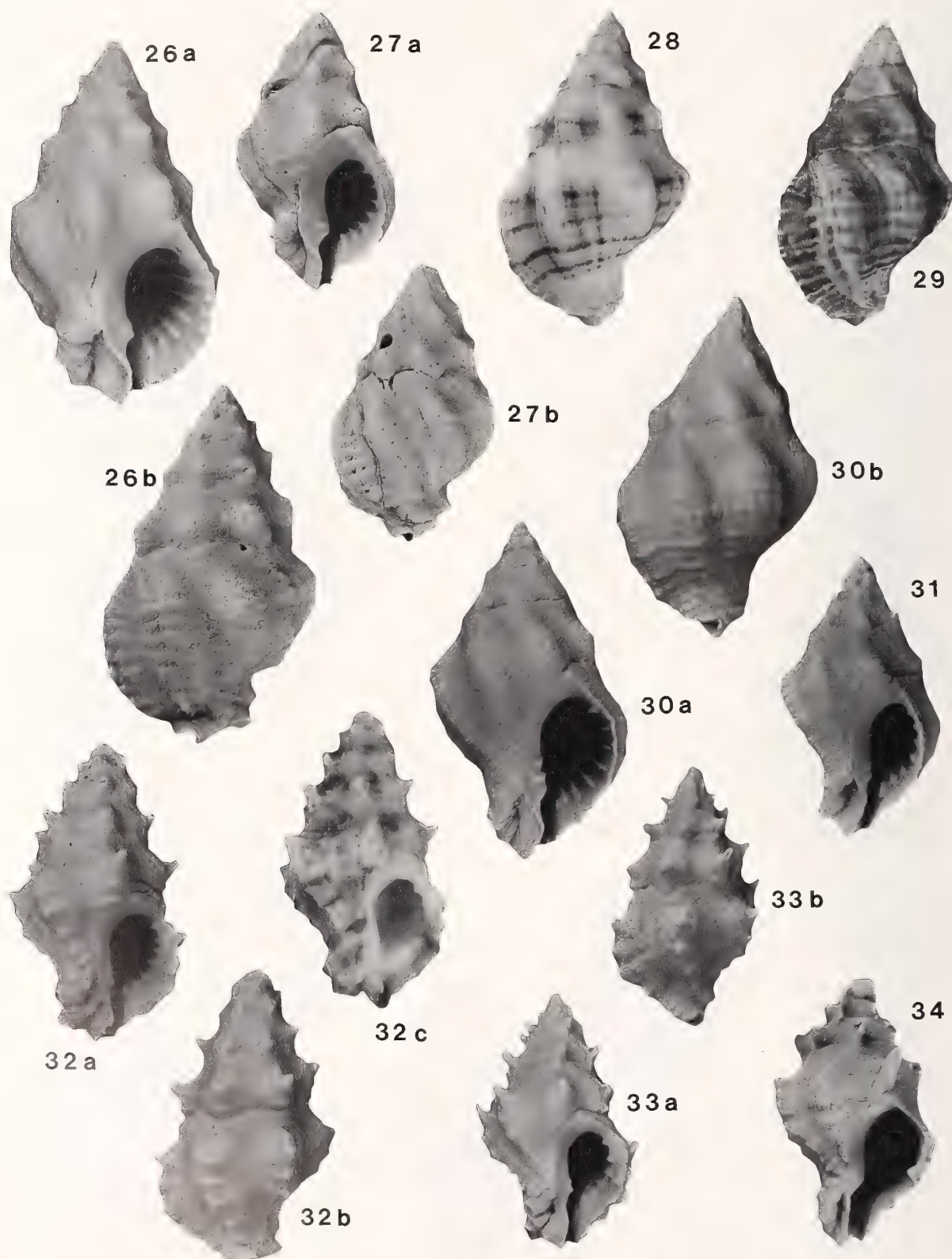
Figure 8. USNM 860299; height 13.9 mm, diameter 8.0 mm; locality: Dominican Republic.

Figure 9. USNM 860298; height 14.3 mm, diameter 9.2 mm; locality: Dominican Republic.

Discussion: This recently described western Atlantic addition to the genus is unique in having a strong color pattern, consisting of a dark brown shell with a white band circling the periphery. As suggested above, it is more similar to the *Chipola* A. *gretae* than to the other living forms and may well represent a different species-complex altogether. At this time, the species is known only from the vicinity of the type locality, where it occurs on and under rocks and coral rubble in depths of 1–5 meters (Petuch, 1993:54).

Explanation of Figures 17 to 25

Figures 17–25. *Attiliosa aldridgei* (Nowell-Usticke, 1969). Figure 17. AMNH 168901 (Paratype); height 22.4 mm, diameter 14.0 mm; locality: Antigua, B.W.I. ×2.5. Figure 18. USNM 890890; height 29.7 mm, diameter 18.3 mm; locality: Bimini, B.W.I., 10 meters (shell not whitened, to show color pattern). ×2. Figure 19a, b. USNM 792393; height 12.3 mm, diameter 8.2 mm; locality: Bimini, B.W.I., 10 meters. Figure 19a ×4; 19b ×10. Figure 20. USNM 890891; height 16.4 mm, diameter 10.5 mm; locality: Discovery Bay, Jamaica, 10 meters (shell not whitened, to show color pattern). ×2.5. Figure 21a, b. USNM 869515; height 19.1 mm, diameter 12.8 mm; locality: TU R-369, Moín, Costa Rica. ×2.5. Figure 22a, b. USNM 489200; height 20.1 mm, diameter 11.7 mm; locality: TU 1422, Cercado Formation. ×2.5. Figure 23a, b. USNM 890892; height 20.7 mm, diameter 12.4 mm; locality: TU R-109, Bahia de Las Minas, Panama. ×2.5. Figure 24a, b. USNM 890893; height 15.1 mm, diameter 9.2 mm; locality: Cartagena, Colombia. ×4. Figure 25. USNM 323924; height 10.8 mm, diameter 6.9 mm; locality: TU 1240, Moín Formation. ×4.



Attiliosa philippiana (Dall, 1889)

(Figures 30, 31)

Muricidea philippiana Dall, 1889:213; 1902:504, pl. 29, fig. 5.*Attiliosa aldrigei* (Nowell-Usticke). Vokes, 1976:in part, pl. 8, fig. 10 only.*Attiliosa philippiana* (Dall). Vokes & D'Attilio, 1982:69; Vokes, 1992:94, pl. 20, fig. 9.

Lectotype: United States National Museum of Natural History, no. USNM 93337; height 14.9 mm, diameter 8.8 mm.

Type locality: U.S. Fish Commission Station 2362, off Cabo Catoche, Quintana Roo, Mexico, in 25 fathoms [46 meters].

Figured specimens:

Figure 30. USNM 890894; height 14.8 mm, diameter 8.5 mm; locality: San Andres Island, Colombia, 15 meters.

Figure 31. USNM 711114; height 10.6 mm, diameter 6.0 mm; locality: TU R-98, Holandes Cay, Panama.

Discussion: For a complete synonymy and history of this misunderstood species, see Vokes & D'Attilio (1982:69). In that discussion it was not noted that one of the specimens figured by Vokes (1976:pl. 8, fig. 10; refigured here, Figure 31) as *A. aldrigei* is actually a juvenile example of *A. philippiana*. Perhaps the misidentification was a result of the belief held at the time that *A. philippiana* was found only in the Florida-Yucatan portion of the western Atlantic (Vokes, 1976:122). But several larger examples (Figure 30) from San Andres Island, taken in 15 meters by SCUBA diver, confirm the presence of this species in the southern Caribbean.

Attiliosa bessei E. H. Vokes, sp. nov.

(Figures 26–29)

Description: Early whorls unknown, all material badly eroded. At least six teleoconch whorls. Axial ornamentation of six or seven rounded ridges on each teleoconch

whorl. Spiral ornamentation very faint, approximately eight cords on body whorl. Suture appressed, sinuated by axial ridges; shoulder sloping. Aperture rounded; columellar lip appressed at posterior end, free-standing at anterior end; smooth except for two or three elongate nodules at anterior end. Outer lip patulous, margin serrated by almost invisible spiral cords, with small adaperturally directed points corresponding to grooves between spiral cords. About seven strong lirae on inner side of outer lip. Siphonal canal short, broad; recurved at distal end, forming a deep, wide siphonal fasciole. Shell invariably coated with coralline algae; when removed, color pattern revealed as variable brown lines topping spiral cords.

Holotype: USNM 880260; height 24.6 mm, diameter 14.5 mm (Figure 26).

Type locality: Rosalind Bank, Bay Islands, Honduras, from 30 meters in lobster traps.

Paratype A: USNM 880261; height 18.8 mm, diameter 11.0 mm; locality same as holotype (Figure 27).

Paratype B: USNM 880262; height 21.6 mm, diameter 12.7 mm; locality: Gorda Banks, Bay Islands, Honduras, from lobster traps (Figure 28).

Paratype C: USNM 880263; height 21.0 mm, diameter 11.9 mm; locality: Gorda Banks, Bay Islands, Honduras, from lobster traps (Figure 29).

Discussion: From the vicinity of the Bay Islands, Honduras, there is a species that is closely related to the more widespread *A. aldrigei*. However, this new species differs from the latter in having a higher spire and shorter siphonal canal, so that the outline of the shell is biconic with the shoulder knobs at the midpoint of the shell height. It is totally lacking in spines, and the color pattern varies from white with numerous thin brown spiral lines (Figure 28) to brown with thin white spiral lines (Figure 29).

This new species is named in honor of Mr. Bruno Bes-

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Explanation of Figures 26 to 34

Figures 26–29. *Attiliosa bessei* E. H. Vokes, sp. nov. Figure 26a, b. USNM 880260 (Holotype); height 24.6 mm, diameter 14.5 mm; locality: Rosalind Bank, Bay Islands, Honduras. ×2.5. Figure 27a, b. USNM 880261 (Paratype A); height 18.8 mm, diameter 11.0 mm; locality: Rosalind Bank, Bay Islands, Honduras. ×2.5. Figure 28. USNM 880262 (Paratype B); height 21.6 mm, diameter 12.7 mm; locality: Gorda Bank, Bay Islands, Honduras (shell not whitened, to show color pattern). ×2.5. Figure 29. USNM 880263 (Paratype C); height 21.0 mm, diameter 11.9 mm; locality: Gorda Bank, Bay Islands, Honduras (shell not whitened, to show color pattern). ×2.5.

Figures 30 and 31. *Attiliosa philippiana* (Dall, 1889). Figure 30a, b. USNM 890894; height 14.8 mm, diameter 8.5 mm; locality:

San Andres Island, Colombia, 15 meters. ×4. Figure 31. USNM 711114; height 10.6 mm, diameter 6.0 mm; locality: TU R-98, Holandes Cay, Panama. ×4.

Figures 32–34. *Attiliosa kevanii* E. H. Vokes, sp. nov. Figure 32a–c. USNM 880264 (Holotype); height 17.9 mm, diameter 11.0 mm; locality: Montego Bay, Jamaica (shell in Fig. 32c not whitened, to show color pattern). ×3. Figure 33a, b. USNM 880265 (Paratype A); height 15.2 mm, diameter 10.1 mm; locality: Montego Bay, Jamaica. ×3. Figure 34. USNM 880266 (Paratype B); height 7.4 mm, diameter 4.3 mm; locality: Utila, Bay Islands, Honduras, 25 meters. ×6.

se, diver in the Bay Islands, who provided much of the available material.

Attiliosa kevani E. H. Vokes, sp. nov.

(Figures 32–34)

Muricopsis pudicus (Reeve). Humfrey, 1975:138, pl. 16, fig. 7 (not of Reeve).

Attiliosa aldridgei (Nowell-Usticke). Vokes, 1992:in part, discussion p. 93 only.

Description: Shell small for genus (maximum height under 18 mm); spire high. Protoconch of one and one-half flattened and tilted whorls (cf. Radwin & D'Attilio, 1976: text-fig. 58—*Prototyphis angasi*); six teleoconch whorls. Axial ornamentation beginning with five small varices on first two teleoconch whorls, increasing to six or seven on later whorls. On first three ornamented whorls each varix with a long, adapically recurved spine at shoulder; spines continuing on later whorls but not as long relative to shell size. No spiral ornamentation visible on spire whorls; on body whorl four faint spiral cords between shoulder and base of whorl; except for varices shell surface almost smooth. Suture appressed, sinuated by varices; shoulder extremely sloping, resulting in spire being almost one-half entire shell height. Aperture rounded, columellar lip expanded and appressed; smooth except for two elongate nodules at anterior end. Outer lip patulous; margin serrated with small adaperturally directed points corresponding to grooves between spiral cords, in immature specimens that one at base of body whorl forming a small sinusigeral projection. Six or seven strong lirae set back from margin of outer lip, extending far into aperture. Siphonal canal short, broad; reflected at distal end, forming a small siphonal fasciole. Color white, with vague brown lines topping spiral cords; some specimens also with broad brown band on shoulder and base of body whorl.

Holotype: USNM 880264; height 17.9 mm, diameter 11.0 mm (Figure 32).

Type locality: Montego Bay, Jamaica, 25 meters.

Paratype A: USNM 880265; height 15.2 mm, diameter 10.1 mm; locality: Montego Bay, Jamaica, 25 meters (Figure 33).

Paratype B: USNM 880266; height 7.4 mm, diameter 4.3 mm; locality: Utila, Bay Islands, Honduras, 25 meters (Figure 34).

Discussion: In a previous discussion of *A. aldridgei*, I stated (Vokes, 1992:93) that the specimen figured by Humfrey (1975:pl. 16, fig. 7) as *Muricopsis pudicus* (Reeve) was certainly not that species, which is a West African *Hexaplex*, but was simply a spinose juvenile specimen of *A. aldridgei*. Furthermore, I noted that in the collection of Kevan and Linda Sunderland, Sunrise, Florida, there were similar juvenile examples taken from 12 to 25 meters depth in the Bay Islands. Since that time numerous adult specimens have been taken by the Sunderlands in both the Bay Islands and Jamaica, and it is now clear that this is a new species, resembling *A. aldridgei* only in the juvenile stages but very different in the adult. According to Mr. Sunderland, this form is always found in old dead reef systems, on algae and always very encrusted with lime, as is typical of other members of the genus *Attiliosa*.

From *A. aldridgei* the new species differs in being smaller (the holotype at just under 18 mm is by far the largest specimen seen) and more spinose. The outline of the shell is less inflated in *A. kevani* and the spire is much higher—almost one-half the total height of the shell.

From the other new species, *A. bessei*, *A. kevani* differs in much the same ways, with *A. bessei* being even less spinose than *A. aldridgei*.

Attiliosa perplexa E. H. Vokes, sp. nov.

(Figures 35–37)

Description: Shell small for genus (maximum height 12 mm), biconic in outline. Protoconch of one and one-half

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Explanation of Figures 35 to 43

Figure 35–37. *Attiliosa perplexa* E. H. Vokes, sp. nov. Figure 35a, b. USNM 880257 (Holotype); height 12.6 mm, diameter 6.8 mm; locality: off Guarapari, Espirito Santo, Brazil, under rocks at 20 meters. $\times 4$. Figure 36a, b. USNM 880258 (Paratype A); height 10.7 mm, diameter 6.3 mm; locality: same as holotype. $\times 4$. Figure 37a, b. USNM 880259 (Paratype B); height 11.4 mm, diameter 6.3 mm; locality: Rasa Island, off Guarapari, Espirito Santo, Brazil, dredged in 30 meters. $\times 4$.

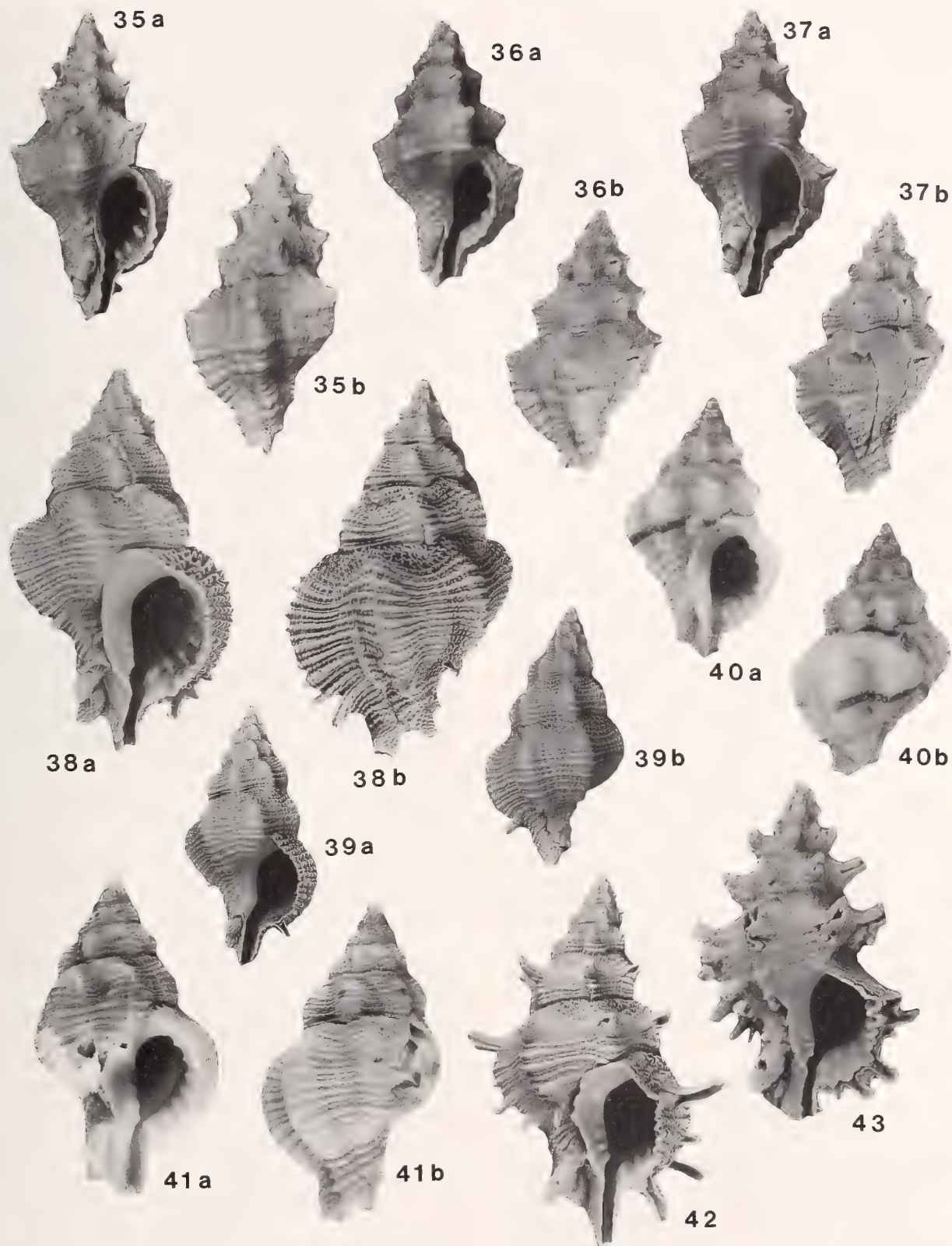
Figures 38 and 39. *Attiliosa houarti* E. H. Vokes, sp. nov. Figure 38a, b. USNM 880255 (Holotype); height 23.5 mm, diameter 12.9 mm; locality: Phuket, Thailand, 30 meters. $\times 2.5$. Figure 39a, b. USNM 880256 (Paratype); height 15.7 mm, diameter 8.3 mm; locality: Kor Bon Island, western Thailand, 12 meters. $\times 3$.

Figure 40a, b. *Attiliosa goreensis* Houart, 1993. MNHN (Holotype); height 14.2 mm, diameter 9.0 mm; locality: Gorée, Senegal, 20–25 meters. $\times 3$.

Figure 41a, b. *Attiliosa bozzettii* Houart, 1993 IRSNB IG27.873/454 (Holotype); height 17.0 mm, diameter 10.1 mm; locality: Ras Hafun, Somalia, 150–200 meters. $\times 3$.

Figure 42. *Attiliosa orri* (Cernohorsky, 1976). USNM 890895; height 30.9 mm; diameter 22.7 mm (including spines); locality: Kantang, Thailand. $\times 2$.

Figure 43. *Attiliosa nodulifera* (Sowerby, 1841). SDSHN 78076a; height 29.0 mm, diameter 20.1 mm; locality: Ataa, Malaita, Solomon Islands. $\times 2$.



smooth, bulbous whorls; six teleoconch whorls. Axial ornamentation of six rounded ridges on each whorl. Spiral ornamentation of flattened cords; four on spire whorls between shoulder and suture; on body whorl two major cords, one at shoulder, one at periphery, approximately 12 secondary cords. Where two major cords cross axial ridges open spines produced, that at shoulder much larger; small open flanges at minor cords. Suture incised; undulated by axial ridges. Aperture elongate-oval; inner lip smooth, appressed; one small nodule at anterior end. Margin of outer lip extended, scalloped by spiral cords; five strong lirae on inner side. Siphonal canal short, broad; recurved at distal end, forming small siphonal fasciole. Outer surface of shell covered by intritacalx; when removed, a single brown spiral band visible at base of body whorl.

Holotype: USNM 880257; height 12.6 mm, diameter 6.8 mm (Figure 35).

Type locality: Off Guarapari, Espirito Santo, Brazil, under rocks at 20 meters.

Paratype A: USNM 880258; height 10.7 mm, diameter 6.3 mm; locality same as holotype (Figure 36).

Paratype B: USNM 880259; height 11.4 mm, diameter 6.3 mm; Rasa Island, off Guarapari, Espirito Santo, dredged in 30 meters (Figure 37).

Discussion: From off the coast of Espirito Santo, Brazil, José and Marcus Coltro have collected a number of specimens of a small species that, although obviously muricine, seemed to defy placement in any recognized genus. The perplexing question of the generic assignment of this unusual new species was first resolved by Mr. Roland Houart, who recognized that *Attiliosa* might be the proper assignment (1995, personal communication). However, in terms of other known members of *Attiliosa*, there is none that bears more than a generic resemblance. The shell is the most attenuated of all *Attiliosa* species, with the height:width ratio more than 2:1. The narrow shell, with a few relatively strong spiral cords, and small size (maximum height about 12 mm) suggests a relationship with the French Miocene *A. sacyi*, and therefore, the species is tentatively included with that species-complex.

Attiliosa goreensis Houart, 1993

(Figure 40)

Attiliosa goreensis Houart, 1993a:20, figs. 11, 12 (holotype), 13 (paratype), 18, 19 (radula), 26, 27 (protoconch).

Holotype: Muséum National d'Histoire Naturelle, Paris; height 14.2 mm, diameter 9.0 mm.

Type locality: Gorée, Senegal, 20–25 meters.

Figured specimen: Holotype (photograph courtesy of Roland Houart).

Discussion: As noted in the original description (Houart, 1993a:21), this species is most closely related to *A. aldridgei* but differs in having more shouldered whorls, with more regular and equi-sized spiral cords. It is also smaller, attaining a maximum size of approximately 15 mm. Interestingly, the holotype (Figure 40) shows a brown spiral band on the body whorl similar (although narrower) to the color form described as *A. poeyana* (cf. Figure 20).

Attiliosa houarti E. H. Vokes, sp. nov.

(Figures 38, 39)

Description: Early whorls unknown, seven teleoconch whorls in adult. Axial ornamentation of six or seven rounded ridges on each teleoconch whorl and multiple growth lamellae covering entire surface of shell. No varical break visible until adult body whorl. Spiral ornamentation of raised cords alternating with smaller threads; approximately 12 major cords on body whorls plus six smaller threads on siphonal canal. Intersection of spiral ornament and growth lamellae giving rise to a scabrous shell surface; on adapertural side of axial ridges lamellae forming small open flanges; that formed by cord at base of body whorl strongest. Suture slightly appressed. Aperture rounded; columellar lip greatly expanded and appressed at posterior end, free-standing at anterior end; smooth, with three small nodules at anterior end. Margin of outer lip serrated by spiral ornamentation, seven elongate nodules on inner side. Siphonal canal short, broad; extremely recurved at distal end with terminations of axial ridges forming small spurs encircling a deep siphonal fasciole. Color uniformly brown; aperture white.

Holotype: USNM 880255; height 23.5 mm, diameter 12.9 mm (Figure 38).

Type locality: Phuket, Thailand, in rubble, 30 meters.

Paratype: USNM 880256; height 15.7 mm, diameter 8.3 mm; Kor Bon Island, western Thailand, 12 meters (Figure 39).

Discussion: Most closely related to *A. bozzettii* Houart, described from the opposite side of the Indian Ocean, *A. houarti* differs from the latter in having a larger aperture and shorter siphonal canal. Both differ from the third Indian Ocean species, *A. orri*, in lacking the extreme development of varical spines seen in that form. Nevertheless, these three Indian Ocean species are more similar to the Atlantic species of the "*A. aldridgei* group" than to the species in the Pacific Ocean.

Attiliosa bozzettii Houart, 1993

(Figure 41)

Attiliosa bozzettii Houart, 1993b:42, figs. 1, 2 (holotype), 3 (paratype), 9 (protoconch).

Holotype: Institut Royal des Sciences Naturelles de Belgique, no. IG27.873/454; height 17.0 mm, diameter 10.1 mm.

Type locality: Ras Hafun, Somalia, 150–200 meters.

Figured specimen: Holotype (photograph courtesy of Roland Houart).

Discussion: There is a strong similarity between three Indian Ocean species of *Attiliosa*. Of these, *A. orri* is the most spinose, *A. houarti* is slightly spinose, and *A. bozzettii* is completely non-spinose. All three share an extremely squamose surface ornamentation. A fourth species, *A. edingeri* Houart, 1998, recently described from the Indian Ocean side of Australia does not seem to be closely related to these three species but rather is a member of the *A. nodulosa* complex.

Attiliosa orri (Cernohorsky, 1976)

(Figure 42)

Muricopsis orri Cernohorsky, 1976:116, figs. 12–20.

Attiliosa orri (Cernohorsky). Vokes & D'Attilio, 1982:71.

Holotype: Auckland Institute and Museum, no. TM-1346; height 27.1 mm, diameter 18.6 (spines excluded).

Type locality: Andaman Islands, Indian Ocean, in 55 meters.

Figured specimen: USNM 890895; height 30.9 mm; diameter 22.7 mm (including spines); locality: Kantang, Thailand.

Discussion: For a complete synonymy see Vokes & D'Attilio (1982:71).

Attiliosa nodulifera (Sowerby, 1841)

(Figure 43)

Murex noduliferus Sowerby, 1841a:8, pl. 194, fig. 94; 1841b:147.

Murex (Trophon) fruticosus Gould, 1849:143.

Murex pagodus A. Adams, 1853:269.

Attiliosa nodulifera (Sowerby). Vokes & D'Attilio, 1982:70, in part, figs. 1–4 (only); D'Attilio & Myers, 1986:62, figs. 8, 9; Houart, 1996:61, fig. 16.

Syntypes: The Natural History Museum, London [British Museum (Natural History)], nos. 1842.5.10 (1618–1619); height of larger (figured by Cernohorsky, 1976: figs. 22, 23) height 20.2 mm, diameter 12.8 mm.

Type locality: Masbate, Philippine Islands.

Figured specimen: SDSNH 78076a; height 29.0 mm, diameter 20.1 mm; locality: Ataa, Malaita, Solomon Islands.

Discussion: According to Cernohorsky (1976:119), the original illustration of *Murex noduliferus* Sowerby, 1841,

is a composite of the two syntypes, a worn mature example (figured by Cernohorsky) and an immature specimen, which better shows the spines.

Attiliosa caledonica (Jousseaume, 1881)

Muricidea caledonica Jousseaume, 1881:349; 1882:345.

Murex (Muricidea) caledonica (Jousseaume). Poirier, 1883: 110, pl. 5, fig. 3 (lectotype; designated by Fischer-Piette and Beigbeder, 1943:206).

"*Muricidea*" *caledonica* (Jousseaume). Vokes & D'Attilio, 1982:68, fig. 5 ("lectotype").

Attiliosa caledonica (Jousseaume). D'Attilio & Myers, 1986:59, figs. 1–7, 10 (fig. 4c = lectotype); Houart, 1996:61, fig. 17; Houart, 1998:96, fig. 31.

Lectotype: Muséum National d'Histoire Naturelle, Paris; height 26.2 mm, diameter 19.0 mm (*vide* D'Attilio and Myers, 1986: fig. 4c).

Type locality: New Caledonia.

Discussion: In our original discussion (Vokes & D'Attilio, 1982:68), we noted the differences between *A. nodulifera* and *A. caledonica* and concluded that the two forms were synonymous. However, D'Attilio & Myers (1986) have presented convincing evidence that the two are indeed distinct species. They also demonstrated that the specimen figured as "lectotype" by Fair (1976:pl. 17, fig. 229) and by Vokes & D'Attilio (1982:fig. 5) was not the specimen figured by Poirier (1883:pl. 5, fig. 3), which had previously been designated as lectotype by Fischer-Piette & Beigbeder (1943:206); in fact, it is not even part of the type lot.

For a complete synonymy of *A. caledonica* see Vokes & D'Attilio (1982:70).

Attiliosa ruthae Houart, 1996

Attiliosa ruthae Houart, 1996:61, figs. 15 (paratype), 31–32 (holotype).

Holotype: Muséum National d'Histoire Naturelle, Paris; height 27.5 mm, diameter 18.1 mm.

Type locality: Cebu, Philippine Islands.

Discussion: This recently described species is most similar to the sympatric *A. nodulifera* but has fringed varices rather than spines.

Attiliosa edingeri Houart, 1998

Attiliosa edingeri Houart, 1998:96, figs. 1, 2 (holotype), 3, 4 (paratypes), 40 (radula).

Holotype: Western Australian Museum, no. WAM S.1101; height 31.9 mm, diameter 18.1 mm.

Type locality: Off Esperance, Western Australia, 31–36 meters.

Discussion: This recently described species is, as noted

by Houart (1998:96), unlike any other known from the Indo-Pacific. In its non-varicate morphology it most nearly resembles the eastern Pacific *A. nodulosa* but differs in having a more scabrous surface ornamentation. The two are also similar in their relatively large size; the largest specimen of *A. edingeri* measures 35.7 mm in height (Houart, 1998:fig. 4), which is only a bit larger than the specimen here figured (Figure 4) of *A. nodulosa*.

Acknowledgments. This study is largely the result of material provided by other persons and I am grateful to all of the friends who contributed specimens and information. In particular, Kevan and Linda Sunderland, Sunrise, Florida, and José and Marcus Coltro, São Paulo, Brazil, have always been extremely generous with Caribbean and Brazilian material; without them this study would not have been possible. Mr. and Mrs. Jack Gibson Smith, Surrey, England, originally provided some of the Venezuelan material, which was later augmented by a loan from Peter Jung, Naturhistorisches Museum, Basel, Switzerland, where the Gibson Smith Collection is now housed. Roger Portell, Florida Museum of Natural History, Gainesville, Florida, sent the unknown specimens from the McGinty Collection for my examination, and Andrew and Greta Murray kindly shared their Chipola material for the new species from those beds. Roland Houart, Landen, Belgium, who loaned me the negatives of his new species of *Attiliosa* that I might reproduce them, over the years has been a valued collaborator in our joint attempts to bring some small degree of order to the Family Muricidae.

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LOCALITY DATA

The following are Tulane University fossil locality numbers:

283. Caloosahatchee Fm. and Bermont Fm. mixed, spoil banks on cross-canal 1.3 miles southwest of Port Charlotte Railroad Station (formerly Murdock) on south side of Florida Highway 771 and Seaboard Airline Railroad (Sec. 12, T. 40 S, R. 21 E), Charlotte County, Florida.
458. Chipola Fm., east bank of Chipola River, above Farley Creek (SW ¼ Sec. 20, T. 1 N, R. 9 W), Calhoun County, Florida.
547. Chipola Fm., west bank of Chipola River, about 2000 feet above Fourmile Creek (SW ¼ Sec. 29, T. 1 N, R. 9 W), Calhoun County, Florida.
548. Chipola Fm., west bank of Chipola River, at bend about 1800 feet south of mouth of Farley Creek (NW ¼ Sec. 29, T. 1 N, R. 9 W), Calhoun County, Florida.
727. Bermont Fm., borrow pits 2.2 miles east of U.S. Highway 27, 15 miles south of South Bay, Palm Beach County, Florida.
817. Chipola Fm., south side of Tenmile Creek, large gully on the property of Mr. A. Sexton (1967) (SE ¼ Sec. 12, T. 1 N, R. 10 W), Calhoun County, Florida.
819. Chipola Fm., Farley Creek, 0.2 mile west of bridge of Florida Highway 275 (SW ¼ Sec. 21, T. 1 N, R. 9 W), Calhoun County, Florida.

999. Chipola Fm., Farley Creek, about 300 yards downstream from bridge of Florida Highway 275 (SW ¼ Sec. 21, T. 1 N, R. 9 W), Calhoun County, Florida.
1196. Chipola Fm., Farley Creek, north bank about 0.8 mile east of bridge on Florida Highway 275 (NE ¼ Sec. 21, T. 1 N, R. 9 W), Calhoun County, Florida.
1215. Gurabo Fm., Rio Gurabo, bluffs on both sides, from the ford on Los Quemados-Sabaneta road, upstream to approximately 1 km above the ford, Dominican Republic.
1240. Moín Fm., Barrio Los Corales, top of hill at end of road that passes Standard Fruit Company box factory, 1.8 km north of main highway at Pueblo Nuevo, which is 2 km west of Puerto Limón, Costa Rica.
1399. Esmeraldas beds, Onzole Fm., roadcut on west side of village of Camarones, which is 20 km (by road) east of bridge over Rio Esmeraldas at Esmeraldas, Prov. of Esmeraldas, Ecuador.
1422. Cercado Fm., Arroyo Bellaco, which is tributary of Rio Cana from the east, coral reef that is exposed for approximately 1 km below the ford at Los Caobas Adentro, 3 km southwest of Las Caobas, Dominican Republic.

The following are Tulane University Recent collecting localities:

- R-98. *Anton Bruun* Cruise 10, dredged in 40 meters northwest of Holandes Cay, and east-northeast of Cape San Blas (9°37'N, 78°50.3'W), Panama.
- R-109. Bahia de las Minas, Isla Payardi, Prov. of Colón, Panama (7000 YBP).
- R-369. Moín Bay, north side of Limón Peninsula; material dredged from bay for fill to make oil terminal (1976), Moín, Costa Rica.
- R-487. Trawled by shrimpers off Guaymas, Sonora, Mexico.

The following is a Florida Museum of Natural History fossil locality number:

- UF CR007. Tamiami Fm., material exposed during construction of "Alligator Alley," 13.3 miles east of Florida Highway 29 (T. 49 S, R. 32 E), Collier County, Florida (TU 797 is same locality).

The following is a Naturhistorisches Museum, Basel, Switzerland, fossil locality number:

- NMB 17530. Mataruca Member, Caujaro Fm., Cementerio de Carrizal, Falcón, Venezuela.

A Systematic Review of the Hydrobiid Snails (Gastropoda: Rissooidea) of the Great Basin, Western United States. Part II. Genera *Colligyrus*, *Eremopyrgus*, *Fluminicola*, *Pristinicola*, and *Tryonia*

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Abstract. This second and final part of a taxonomic treatment of hydrobiid snails of the Great Basin region in the western United States (based principally on material collected during a recently completed field survey) focuses on fauna other than the genus *Pyrgulopsis*. A new genus of small amnicoline snails, *Colligyrus*, is proposed for *Hydrobia greggi* Pilsbry, 1935, together with a new species from the Harney Lake basin of Oregon. This group is strongly differentiated from other amnicolines by a unique female genitalic groundplan. New records are provided for three species of *Fluminicola*, and two new congeners are described from the northwest Great Basin, both of which had previously been confused with *F. turbiniformis* (Tryon, 1865). A new genus of cochliopine snails, *Eremopyrgus*, is erected for a new species from Steptoe Valley, Nevada. *Eremopyrgus* is distinguished from other cochliopines by unique aspects of its glandular penial lobes and other genitalic features. New records are provided for two species of *Tryonia*, and a new congener is described from thermal springs in central Nevada. Several new records of *Pristinicola hemphilli* (Pilsbry, 1890) from the extreme northwest Great Basin are provided.

INTRODUCTION

In the first part of a systematic review of hydrobiid snails of the Great Basin in the western United States (based principally on material collected during a recently completed field survey), 58 new species belonging to the widespread genus *Pyrgulopsis* were described, and new records were provided for 10 previously described congeners (Hershler, 1998). In this second and final part of this review, other hydrobiid groups, which are much more modestly represented in the region, are similarly treated. Novelties described herein include two small species of *Fluminicola* from the northwest Great Basin previously confused with *F. turbiniformis* (Tryon, 1865), a species of *Tryonia* from central Nevada, a new genus of cochliopine snails from eastern Nevada, and a new genus of small amnicoline snails from northern segments of the Great Basin.

The reader is referred to Hershler (1998) for study rationale and methodology. Institutional repositories of examined specimens are indicated by the following abbreviations: ANSP, Academy of Natural Sciences, Philadelphia; CAS, California Academy of Sciences, San Francisco; FMNH, Field Museum of Natural History, Chicago; USNM, former United States National Museum, collections now in National Museum of Natural History, Smithsonian Institution, Washington, D.C. Shell parameters for new species are summarized in Table 1.

SYSTEMATICS

Family HYDROBIIDAE Troschel, 1857

Colligyrus, Hershler, gen. nov.

Type species: *Hydrobia greggi* Pilsbry, 1935. Also included is *Colligyrus depressus*, sp. nov. (described below).

Etymology: From New Latin, *collis*, hill or high ground; and *gyrus*, circle or round. Referring to the upland habitat and coiled shell of these snails. Gender masculine.

Diagnosis: A northwestern American amnicoline group having a small, globose to conical shell and paucispiral operculum. Female coiled oviduct simple; glandular oviduct large, ventrally closed; bursa copulatrix large, posteriorly positioned; seminal receptacles, 2.

Description: Shell small (up to 3.3 mm in length), thin, globose to conical, umbilicate. Whorls, 3.5–4.5, convex, narrowly shouldered, sutures impressed. Shell clear to white, periostracum thin. Shell apex nearly flat; protoconch of about 1.5 whorls, sculptured with weak spiral lineations. Teleoconch smooth except for faint growth lines. Aperture medium-sized, ovate or circular; outer lip thin; parietal lip complete across body whorl, thin; columellar lip sometimes slightly thickened. Umbilicus narrow to perforate. Operculum flat, thin, ovate, paucispiral. Outer margin of operculum without rim; attachment scar and callus weakly developed. Body pigmentation well de-

Table 1

Selected shell parameters for new species. Data expressed as mean with standard deviation given below. Measurements are given in mm. *n* = number of specimens, μ = mean, SD = standard deviation, SH = shell height, SW = shell width, HBW = height of body whorl, WBW = width of body whorl, AH = aperture height, AW = aperture width, SS = shell width/shell height, WH = number of shell whorls.

		SH	SW	HBW	WBW	AH	AW	SS	WH
<i>Colligyrus depressus</i>									
USNM 860756	μ	1.98	1.78	1.73	1.52	1.05	0.93	0.90	3.60
<i>n</i> = 15	SD	0.05	0.06	0.04	0.03	0.05	0.04	0.03	0.13
<i>Fluminicola insolitus</i>									
USNM 860757	μ	4.55	3.86	3.88	3.13	2.59	2.30	0.85	3.78
<i>n</i> = 13	SD	0.25	0.18	0.18	0.17	0.12	0.15	0.03	0.09
<i>Fluminicola virginius</i>									
USNM 874902	μ	3.19	2.85	2.81	2.08	1.88	1.64	0.89	3.48
<i>n</i> = 15	SD	0.13	0.08	0.11	0.08	0.10	0.09	0.03	0.22
<i>Eremopyrgus eganensis</i>									
USNM 874692	μ	3.44	1.89	2.35	1.71	1.57	0.96	0.55	4.78
<i>n</i> = 15	SD	0.21	0.09	0.11	0.07	0.12	0.05	0.02	0.23
<i>Tryonia monitorae</i>									
USNM 892046	μ	3.87	1.39	1.72	1.34	1.04	0.71	0.36	7.02
<i>n</i> = 15	SD	0.19	0.07	0.10	0.07	0.05	0.05	0.01	0.20
USNM 874882	μ	3.87	1.38	1.68	1.30	1.01	0.67	0.36	6.98
<i>n</i> = 14	SD	0.28	0.08	0.09	0.08	0.06	0.05	0.02	0.32

veloped. Salivary glands long, simple tubes. Radula ribbon elongate (ca. 15 times longer than wide), coiled behind buccal mass. Cutting edge of central teeth straight or weakly concave, bearing 9–15 short cusps. Central cusp pointed, slightly larger than lateral cusps. Basal cusps, 1–2 (sometimes absent on one side), innermost cusp largest. Lateral margins of central teeth angled about 40° to vertical axis of tooth, slightly thickened, distally expanded, projecting slightly beyond V-shaped base of tooth. Lateral teeth with 2–4 inner cusps and 3–5 outer cusps; basal process well developed. Lateral wing of lateral teeth rather broad, somewhat longer than cutting edge. Marginal teeth with relatively numerous cusps; cusps on inner marginals larger than those on outer marginals. Dorsal folds of esophagus short, straight. Cephalic tentacles medium length in preserved material. Ctenidium absent, reduced to a vestige, or well developed, with small, triangular filaments. Osphradium medium-sized, narrow. Hypobranchial gland well developed along rectum. Renal organ with prominent pallial bulge. Stomach longer than style sac, posterior caecal appendix absent; anterior stomach chamber larger than posterior chamber. Rectum straight in pallial roof. Cephalo-pedal ganglia weakly pigmented; cerebral and pedal commissures short. Testis large. Prostate gland small, walls of medium thickness. Penis small to medium-sized relative to head, bifurcate. Lobe slightly shorter than filament, arising from inner edge at or near base, usually posteriorly oriented, weakly folded along most of length. Lobe containing weakly coiled duct which enters small muscular sac distally and exits as eversible papilla through cup-shaped

opening. Duct exits base of lobe into nuchal cavity, broadening to form a large mass of blindly ending glandular loops above the salivary glands; gland lined with thin muscular coat. Penial filament straight or coiled to left, tapering to pointed tip. Penial duct medium width, with thick muscular coat, straight or weakly undulating basally, positioned along outer edge of filament. Females oviparous. Ovary small. Glandular oviduct consisting of sub-equal albumen and capsule glands. Albumen gland with short pallial component. Coiled oviduct a single, posteriorly arched loop opening to anterior portion of albumen gland. Bursa copulatrix medium-sized, positioned posteriorly, partly overlapped by albumen gland. Bursal duct ciliated, short to medium length, originating from anterior edge, opening to oviduct slightly behind pallial wall. Posterior seminal receptacle pouchlike, opening to distal arm of coiled oviduct; anterior seminal receptacle ovate to circular, pressed against ventral edge of albumen gland, opening to oviduct just distal to connection with bursal duct. Capsule gland with narrow, vertical lumen. Sperm tube narrow, separated from capsule gland along most of length, but distally fused to form common genital aperture.

Remarks: The small anterior female accessory pouch has a cellular structure similar to that of the posterior seminal receptacle and, although sperm was not seen in sectioned material, the pouch nevertheless is interpreted as a seminal receptacle. *Colligyrus* differs from other amnicolines in that females have three sperm pouches: a posterior bursa copulatrix and two small seminal receptacles. In con-

trast, a group composed of *Dasyscias*, *Lyogyrus*, and *Parabythinella* has but a single, posterior sperm pouch (e.g., Thompson & Hershler, 1991:fig. 11 [*Dasyscias franzi* Thompson & Hershler, 1991]), which represents a bursa copulatrix based on its columnar cell lining and absence of oriented sperm in its lumen (Hershler, unpublished); while a second group composed of *Amnicola* and *Marstoniopsis* has a posterior bursa copulatrix and a single large seminal receptacle (e.g., Hershler & Thompson, 1988:fig. 8 [*Amnicola limosa* (Say, 1817)]).

Although the type species of *Colligyus* resembles *Lyogyrus* (to which it was most recently allocated) in its diminutive conical shell, *Colligyus* nevertheless is more similar to *Amnicola* in female genitalic groundplan, although it differs in having two (as opposed to a single) seminal receptacles. *Colligyus* and *Amnicola* have a weaker protoconch microsculpture than *Lyogyrus* and also share a paucispiral (as opposed to multispiral) operculum. The anterior seminal receptacle of *Colligyus* may be homologous to that of *Amnicola*, as both of these sacs open to the oviduct distal to the coiled portion at or near the junction of the bursal duct (the posterior seminal receptacle of *Colligyus* opens to the distal arm of the coiled oviduct as in most hydrobiids). Note, however, that these sacs otherwise differ in their size, shape, and position. *Colligyus* also differs from *Amnicola* in having diffuse rather than banded pigment on the dorsal surface of the mantle, a much more elongate radula, narrower central cusps on the central and lateral radular teeth, more numerous cusps on the marginal radular teeth, and a more basal position of the penial lobe.

Colligyus lives in cold springs and spring runs in the upper Snake River basin and northeastern (Bonneville basin) and northwestern (Harney Lake basin) portions of the Great Basin.

Colligyus greggi (Pilsbry, 1935)

(Figures 1, 2A–D, 3A, 5)

Hydrobia greggi Pilsbry, 1935:93–94, fig. 2.—Henderson, 1936:138, fig. 9.—Baker, 1964:173.—Beetle, 1957:19.—Beetle, 1961:5.—Beetle, 1989:639.

Amnicola greggi (Pilsbry, 1935), Taylor, 1966b:173.—Taylor, 1975:90 (literature compilation).—Turgeon et al., 1988:60.

Amnicola (Lyogyrus) greggi (Pilsbry, 1935), Burch & Tottenham, 1980:124, figs. 292, 303.

Diagnosis: Small to medium-sized, with conical shell.

Description: Shell (Figure 1A) conical; height, 1.7–3.3 mm; whorls, 3.75–4.5. Protoconch (Figure 1B, C) of about 1.5 whorls, diameter about 0.49 mm; microsculpture of numerous weakly incised spiral lineations. Teleoconch whorls weakly convex, adapical shoulder often well developed. Shell clear to white, often transparent. Periostracum light brown or tan. Aperture ovate or circular, without adapical angulation. Outer lip weakly prosocline, thin to moderately thick. Parietal lip narrowly adnate to well separated from body whorl. Umbilicus narrow to perforate; columellar swelling absent to narrow.

Operculum (Figure 1D, E) light amber; outer margin without rim, dorsal surface weakly frilled. Attachment scar slightly thickened all around, especially along inner edge. Callus weakly developed.

Radula with about 155 rows of teeth; ribbon length, 1.5 mm, ribbon width, 94 μ m; central tooth width, 25 μ m. Cutting edge of central tooth (Figure 1F) straight or very weakly indented; lateral cusps, 4–7; median cusp pointed, slightly broader and longer than laterals; basal cusps, 1–2; basal tongue narrowly triangular, even with or slightly shorter than lateral margins, basal sockets moderately excavated. Lateral tooth (Figure 1G) with slightly convex dorsal edge; lateral wing longer (150%) than cutting edge; tooth face taller than broad; central cusp weakly pointed, lateral cusps, 2–4 (inner), 3–4 (outer). Inner marginal teeth (Figure 1H) with 24–27 cusps; outer marginal teeth (Figure 1I) with 25–33 cusps.

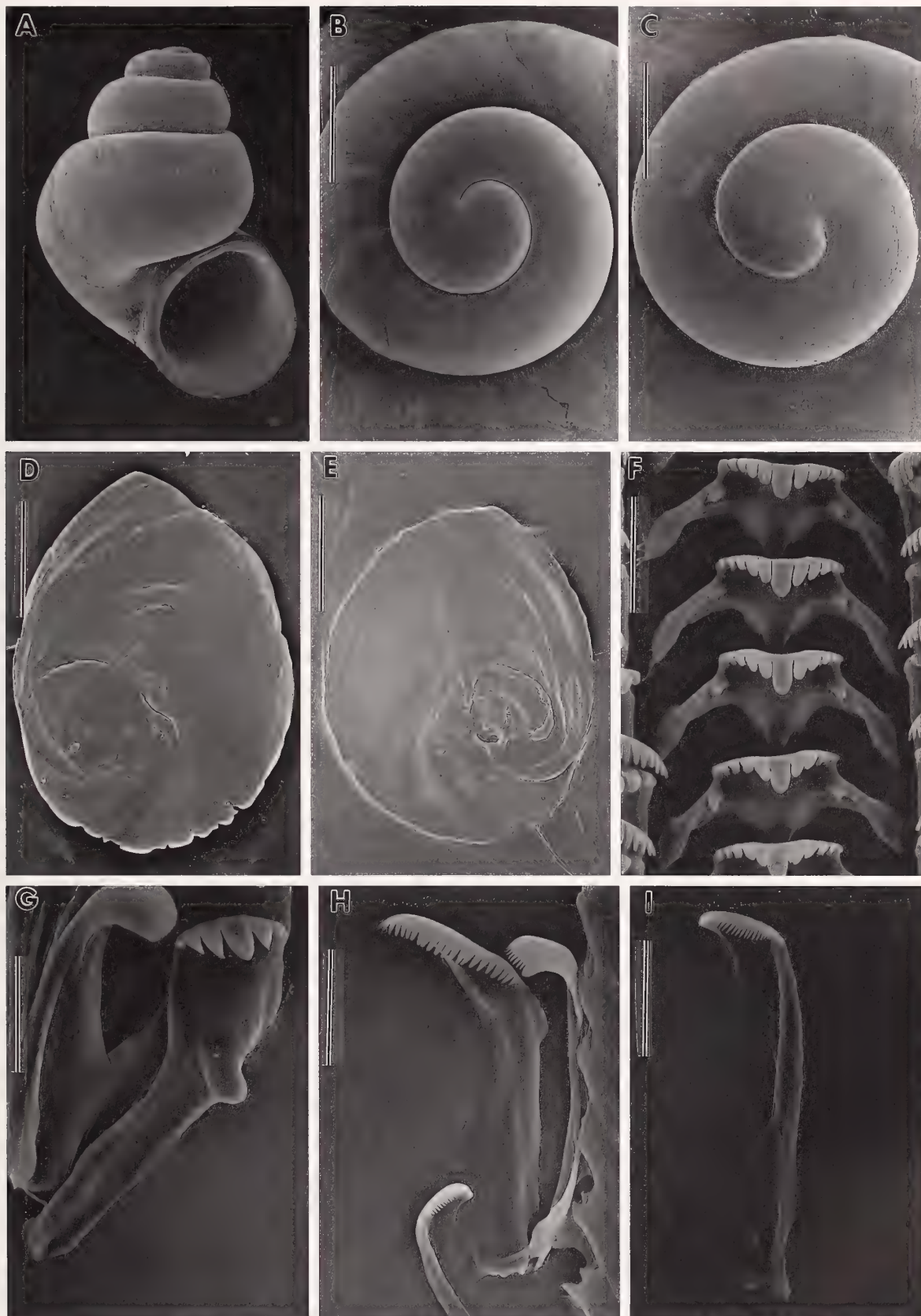
Tentacles light gray to black. Snout light gray. Foot pale, opercular pale or fringed with medium gray pigment. Neck pale or pigmented with scattered gray granules. Pallial roof, visceral coil black.

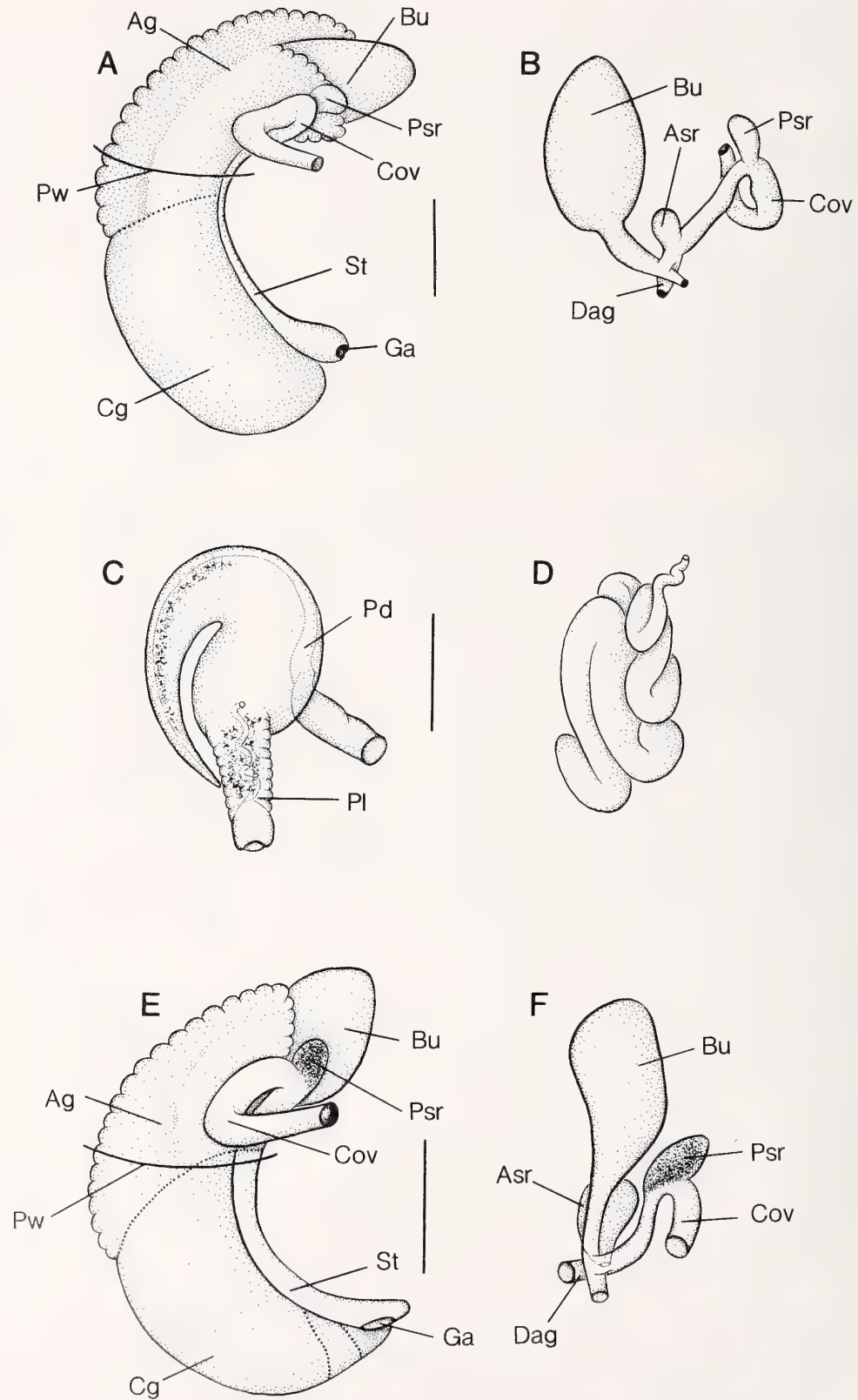
Ctenidium well developed, slightly overlapping pericardium; filaments about 17, small, about as tall as wide, weakly pleated. Osphradium about 33% of ctenidium length, positioned centrally or slightly posterior to middle of ctenidium.

Ovary slightly less than 0.5 whorl, abutting posterior edge of stomach, filling less than 50% of digestive gland behind stomach. Distal female genitalia shown in Figure 2A, B. Bursa copulatrix about 67% of length of albumen gland; narrowly ovate, horizontal, with about half of length overlapped by albumen gland. Bursal duct short (about 33% of length of bursa copulatrix), distinctly nar-

Figure 1

Scanning electron micrographs of shell, operculum, and radula of *Colligyus greggi* Hershler, gen. nov., USNM 883531. A. Shell (height 2.3 mm). B, C. Shell apex. Bars = 200 μ m, 160 μ m, respectively. D. Operculum, outer surface. Bar = 270 μ m. E. Operculum, inner surface. Bar = 285 μ m. F. Central radular teeth. Bar = 12 μ m. G. Lateral radular tooth. Bar = 13 μ m. H. Inner marginal tooth. Bar = 13 μ m. I. Outer marginal tooth. Bar = 12.5 μ m.





rower than bursa copulatrix. Posterior seminal receptacle a small, ovate sac (with short duct) overlapping the bursa copulatrix, sometimes overlapped anteriorly by albumen gland. Posterior seminal receptacle abutting the posterior edge of the coiled oviduct, opening to the postero-ventral edge of this duct. Anterior seminal receptacle a somewhat smaller, nearly circular sac; duct absent or very short. Albumen gland with a weak rectal furrow; furrow absent on capsule gland. Albumen gland with short (20%) pallial component. Capsule gland about as long and wide as albumen gland. Anterior portion of sperm tube expanded into vestibule; genital opening a small, terminal pore.

Testis 1.25 whorls, filling more than 50% of digestive gland behind stomach. Prostate gland bean-shaped, with about 38% of length in pallial roof. Distal vas deferens a broad, thickened tube, slightly undulating in pallial roof and neck. Penis shown in Figure 2C; tubular gland shown in Figure 2D. Penial lobe arising from base. Penial duct narrowing somewhat in base of penis; undulating basally, otherwise straight. Penis pigmented with scattered internal granules; base sometimes darkly pigmented with melanin.

Type locality: Cliff Creek canyon, a fork of Hoback Canyon, about 29 miles (46 km) south of Jackson, Wyoming, in the Snake River drainage. The type locality has not been precisely located. A spring in Cliff Creek canyon harboring this species is shown in Figure 4A. Lectotype, ANSP 163812 (Figure 3A); paralectotypes, ANSP 375735. Baker (1964) separated the single figured specimen and identified this as the "type by original measurement," which is construed as a lectotype designation.

Remarks: This snail lives in the upper Snake River basin and northeastern corner of the Great Basin (Bonneville basin) (Figure 5). Records from western Montana (Taylor 1966b:173) require confirmation. Populations assigned to this species vary slightly in shell shape, relationship between aperture and body whorl, and thickness of shell lip. Taylor (1966b:173) reported laminate egg capsules (typical of amnicoline snails) for this species.

Material examined: IDAHO. *Bannock County*: Heart Mtn. Spring, Marsh Valley, T. 13 S, R. 39 E, NW ¼ section 2, USNM 883881. *Bear Lake County*: spring,

Right Fork Georgetown Canyon, Bear River drainage, T. 11 S, R. 44 E, NW ¼ section 10, USNM 883522.—spring, Home Canyon, Bear River drainage, T. 12 S, R. 45 E, NW ¼ section 32, USNM 883524. *Caribou County*: Harris Spring complex, Bear River drainage, T. 11 S, R. 41 E, NE ¼ section 9, USNM 883394.—Kackley Spring, Bear River drainage, T. 10 S, R. 40 E, SW ¼ section 21, USNM 883539.—spring, Kelly Park, Soda Springs, Bear River drainage, T. 9 S, R. 42 E, NW ¼ section 5, USNM 883523. *Franklin County*: spring, Cottonwood Creek, Bear River drainage, T. 12 S, R. 39 E, NE ¼ section 25, USNM 883392. **UTAH.** *Cache County*: China Row Spring, Logan Canyon, Cache Valley, T. 12 N, R. 3 E, NE ¼ section 7, USNM 858288, USNM 883393.—spring, east of Porcupine Reservoir, Cache Valley, T. 9 N, R. 2 E, NW ¼ section 17, USNM 883880. **WYOMING.** *Lincoln County*: spring, Sublette Creek, Bear River drainage, T. 24 N, R. 118 W, NW ¼ section 8, USNM 883396.—spring, Salt Creek, Bear River drainage, T. 29 N, R. 119 W, SW ¼ section 24, USNM 883395. *Sublette County*: spring, Cliff Creek, Snake River drainage, T. 38 N, R. 114 W, NW ¼ section 23, USNM 883531.

Colligyrus depressus Hershler, sp. nov.

Harney Basin dusksnail
(Figures 2E, F, 3B, 5, 6)

Etymology: from New Latin, *depressus*, meaning pressed down, low, and referring to the squat shell of this species.

Diagnosis: Small, with globose to low-conic shell.

Description: Shell (Figure 6A) low-conic, rarely with eroded spire; height, 1.9–2.1 mm; whorls, 3.5–3.75. Apex often inclined; protoconch (Figure 6B, C) of 1.4–1.5 whorls, diameter about 0.44 mm; microsculpture of numerous weak spiral lineations. Teleoconch whorls convex, often markedly so, narrowly shouldered. Shell clear to white, translucent. Periostracum tan. Aperture medium-sized, ovate, weakly angled adapically. Outer lip prosocline, weakly sinuate (adapically advanced). Parietal lip narrowly adnate to or slightly separated from body whorl; columellar lip without swelling. Umbilicus perforate.

←

Figure 2

Genitalia of *Colligyrus* Hershler, gen. nov., species (A–D, *C. greggi*, USNM 883531; E, F, *C. depressus* Hershler, gen. & sp. nov., USNM 860756). A. Left side of female glandular oviduct and associated structures. Bar = 0.5 mm. B. Bursa copulatrix and associated structures. Scale as in "A." C. Dorsal surface of penis. Bar = 0.25 mm. D. Tubular gland (coiled within cephalic haemocoel). Scale as in "C." E. Left side of female glandular oviduct and associated structures. Bar = 0.25 mm. F. Bursa copulatrix and associated structures. Scale as in "E." Ag, albumen gland; Asr, anterior seminal receptacle; Bu, bursa copulatrix; Cg, capsule gland; Cov, coiled oviduct; Dag, opening of oviduct to albumen gland; Ga, genital aperture; Pd, penial duct; Psr, posterior seminal receptacle; Pw, posterior wall of pallial cavity; St, sperm tube.

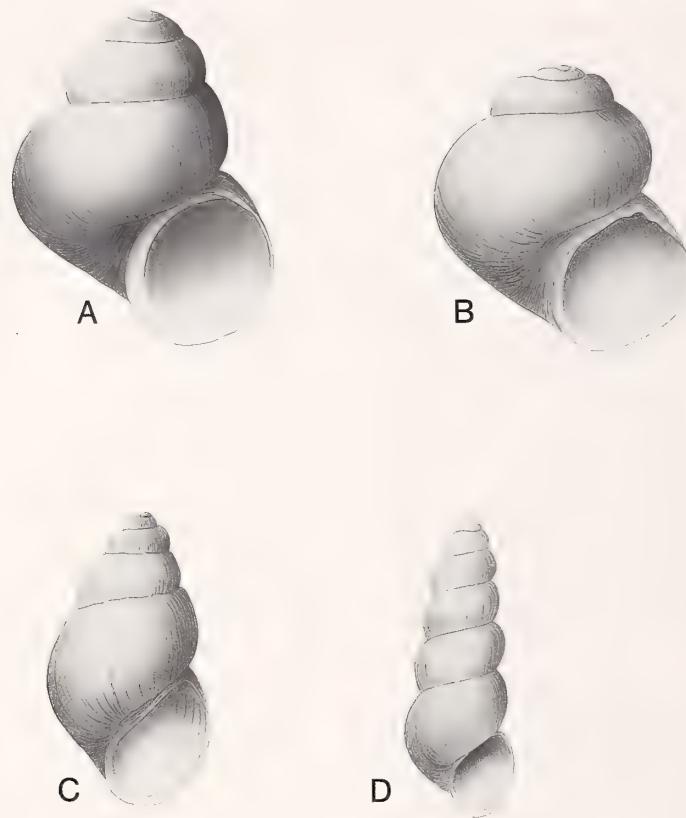


Figure 3

Type material of Great Basin species of *Colligyrus* Hershler, gen. nov., *Eremopyrgus* Hershler, gen. nov., and *Tryonia*. A. *C. greggi*, lectotype, ANSP 163812 (shell height 2.6 mm). B. *C. depressus* Hershler, gen. & sp. nov., holotype, USNM 883876 (1.7 mm). C. *E. eganensis* Hershler, gen. & sp. nov., holotype, USNM 874692 (3.1 mm). D. *T. monitorae* Hershler, sp. nov., holotype, USNM 892046 (3.0 mm).

Operculum (Figure 6D, E) brown in nuclear region, otherwise clear; outer margin without rim. Attachment scar margin slightly thickened along inner edge. Callus weakly developed in nuclear region.

Radula with about 170 rows of teeth; ribbon length, 1.4 mm, ribbon width, 88 μ m; central tooth width, 22 μ m. Cutting edge of central tooth (Figure 6F) weakly to

moderately indented; lateral cusps, 6–7; median cusp rounded or weakly pointed, slightly broader and longer than laterals; basal cusps, 1, sometimes absent on one side; basal tongue slightly shorter than lateral margins, basal sockets deeply excavated. Lateral tooth (Figure 6G) with horizontal or slightly convex cutting edge; lateral wing slightly longer (125%) than cutting edge; tooth face

Figure 4

Type and other localities for species treated herein. A. Spring, Cliff Creek, Snake River drainage, Sublette County, Wyoming. Habitat of *Colligyrus greggi* Hershler, gen. nov. in vicinity of type locality. Photograph, September, 1993. B. Springs, Cricket Creek, Silvies River drainage, Harney County, Oregon. Type locality of *C. depressus* Hershler, gen. & sp. nov. Photograph (D. Sada), July, 1994. C. Page Springs, Donner und Blitzen River drainage, Harney County, Oregon. Type locality of *Fluminicola insolitus* Hershler, sp. nov. Photograph (D. Sada), July, 1993. D. "Waterfall" spring, source of Hardscrabble Creek, Pyramid Lake basin, Washoe County, Nevada. Type locality of *F. virginus* Hershler, sp. nov. Photograph (G. Vinyard), October, 1992. E. Spring northwest of Clark Spring, Steptoe Valley, White Pine County, Nevada. Type locality of *Eremopyrgus eganensis* Hershler, gen. & sp. nov. Photograph, June, 1992. F. Hot Springs, Potts Ranch, Monitor Valley, Nye County, Nevada. Type locality of *T. monitorae* Hershler, sp. nov. Photograph (D. Sada), November, 1992. G. Dianas Punch Bowl (Hot Springs), Monitor Valley, Nye County, Nevada. Habitat of *T. monitorae* Hershler, sp. nov. Photograph (D. Sada), November, 1992.



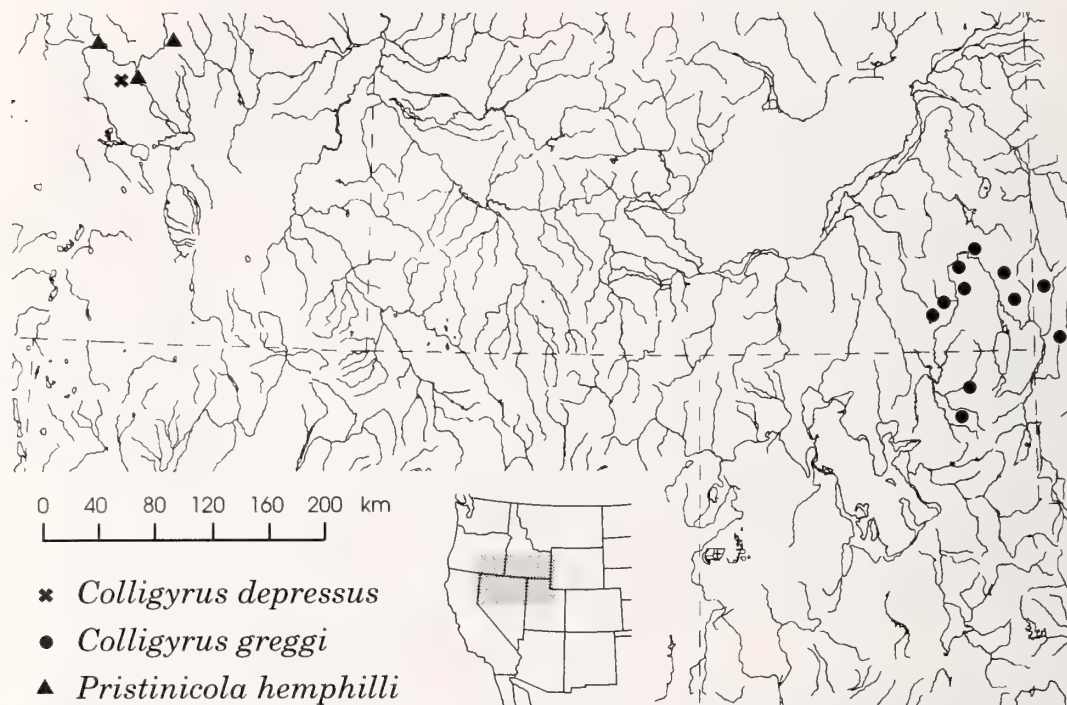


Figure 5

Map of northern Great Basin and adjacent regions showing the distribution of *Colligyryus* Hershler, gen. nov. species and *Pristinicola hemphilli*. Previously reported localities for *Pristinicola hemphilli* (see Hershler et al., 1994) are not shown.

taller than broad; central cusp rounded, lateral cusps, 3 (inner), 4–5 (outer). Inner marginal teeth (Figure 6H) with 26–30 cusps; outer marginal teeth (Figure 6I) with 25–29 cusps.

Snout, tentacles, foot light to medium gray. Inner edge of opercular lobe black. Neck unpigmented to medium gray. Pallial roof, visceral coil medium gray to black.

Ctendium absent or represented by a few (3–6) small, stubby vestiges; branchial vessel not seen in dissection. Osphradium anteriorly positioned, filling about 20% of pallial cavity length.

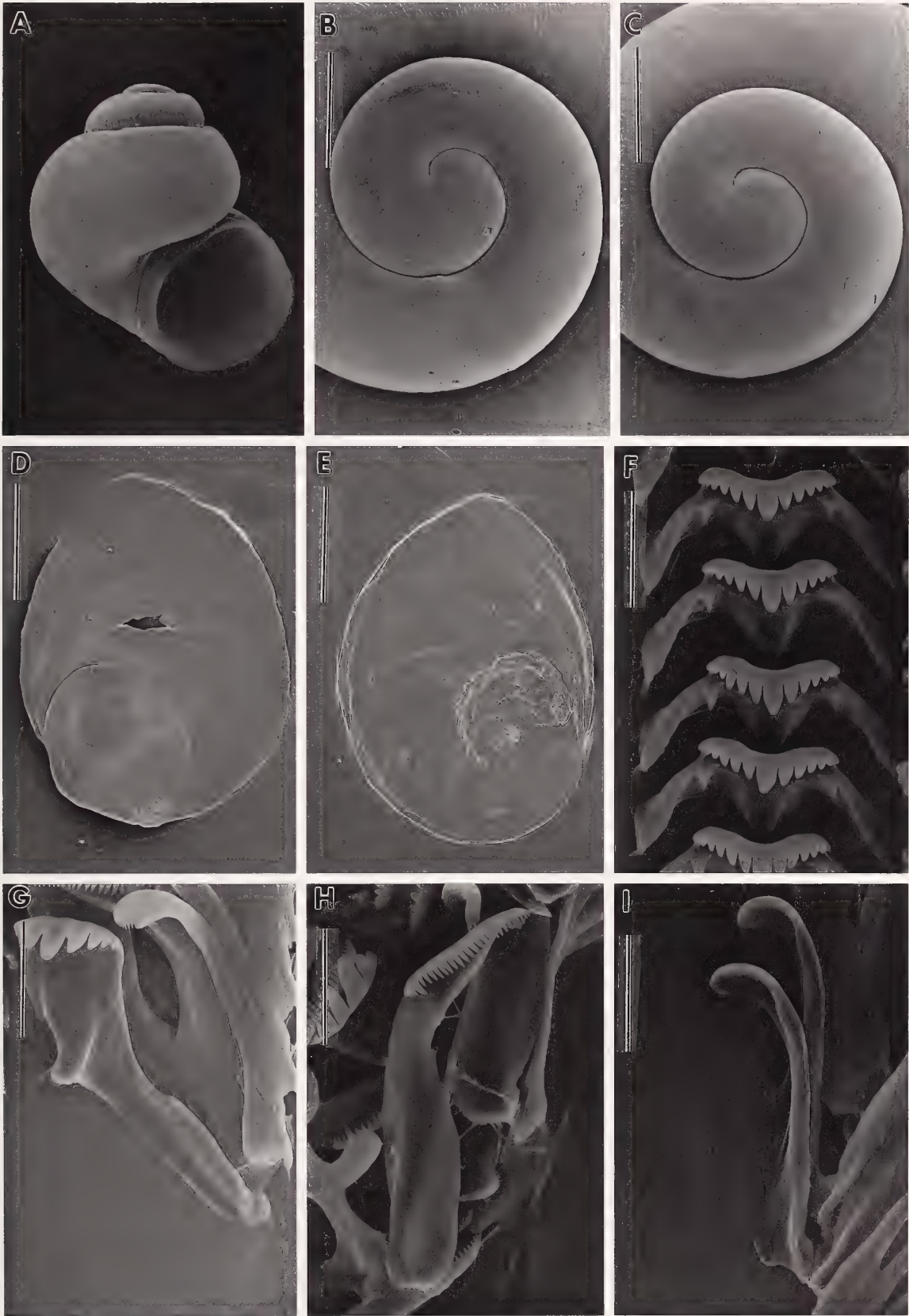
Ovary about 0.5 whorl, abutting or slightly overlapping posterior stomach chamber, filling less than 50% of digestive gland behind stomach. Distal female genitalia shown in Figure 2E, F. Bursa copulatrix about 50% of albumen gland length; ovate or clublike, horizontal or

obliquely oriented, about 50% overlapped by albumen gland. Bursal duct medium length (50–67% of bursa length), often narrow, sometimes poorly distinguished from bursa. Posterior seminal receptacle small, without duct, overlapping anterior half of bursa copulatrix, positioned near ventral edge of albumen gland. Portions of coiled oviduct adjacent to posterior seminal receptacle often filled with sperm. Anterior seminal receptacle disc-shaped. Albumen gland with weak rectal furrow. Albumen gland with short (about 22%) pallial section; capsule gland entirely pallial, composed of two distinct glandular units. Genital opening a small terminal slit.

Testis 1.0–1.25 whorl, broadly overlapping stomach chambers, filling about 50% of digestive gland behind stomach. Prostate gland ovate, entirely visceral. Pallial vas deferens a broad tube without bends or undulations;

Figure 6

Scanning electron micrographs of shell, operculum, and radula of *Colligyryus depressus* Hershler, gen. & sp. nov. USNM 860756. A. Shell (height 1.8 mm). B, C. Shell apex. Bars = 170 μ m, 188 μ m, respectively. D. Operculum, outer surface. Bar = 230 μ m. E. Operculum, inner surface. Bar = 240 μ m. F. Central radular teeth. Bar = 10 μ m. G. Lateral radular tooth. Bar = 13 μ m. H. Inner marginal tooth. Bar = 12.5 μ m. I. Outer marginal teeth. Bar = 11.5 μ m.



portion of vas deferens in neck straight. Penial lobe arising slightly distal to base. Penial duct narrow throughout. Penis unpigmented.

Type locality: Unnamed springs, Cricket Creek, Silvies River drainage, Harney County, Oregon, T. 21 S, R. 28 E, NW ¼ section 12. The type locality is composed of a series of small, cold rheocrenes (11°C, 81 micromhos/cm) (Figure 4B). Holotype, USNM 883876 (Figure 3B); paratypes, USNM 860756.

Remarks: *Colligyrus depressus* is thus far known only from the type locality in southeast Oregon (Figure 5). This species differs from *C. greggi* in its broader shell, absence or vestigial nature of ctenidium, more distal position of penial lobe, longer bursal duct, discoidal shape of the anterior seminal receptacle, division of capsule gland into two distinct units, and slitlike female genital aperture.

Material examined: OREGON. Harney County: springs, Cricket Creek, Silvies River drainage, USNM 860756, USNM 883876.

Fluminicola Carpenter, 1864

Type species: *Paludina nuttalliana* Lea, 1838; original designation.

Diagnosis: A morphologically diverse group of north-western North American lithoglyphine snails.

Remarks: *Fluminicola* and its species recently were reviewed by Hershler & Frest (1996). This genus, as currently constituted, is paraphyletic (Hershler & Frest, 1996:fig. 3), but a confident resolution of its systematics must await a more complete study of the type species, for which anatomical material is not available and which may now be extinct owing to urban development along the lower reach of the Willamette River (type locality area).

Fluminicola coloradensis Morrison, 1940

(Figures 7, 8A–C)

Fluminicola fusca (Haldeman, 1841), Binney, 1865:92 (in part).—Call, 1884:21 (in part).—Pilsbry, 1899:123 (in part).—Hannibal, 1912:187 (in part).—Henderson, 1924:192 (in part).—Chamberlin & Jones, 1929:180–181, fig. 84 (in part; numerous Utah localities).—Henderson, 1936:139.—Jones, 1940:41 (in part).—Baily & Baily, 1951:50 (in part).—*Fluminicola seminalis* (Hinds, 1842), Chamberlin & Jones, 1929:179–180 (in part).

Fluminicola coloradoense Morrison, 1940:125.—Hershler & Frest, 1996:8–9, figs. 1A–E, 2, 4A, 5A–D, 6A, 7A, 8A–C, 9A, 10A, 11.

Lithoglyphus hindsii (Baird, 1863), Taylor, 1966a:fig. 14 (in part).—Taylor, 1985:306 (Green River).—Taylor & Bright, 1987:249 (in part).

Fluminicola hindsii (Baird, 1863), Burch & Tottenham, 1980:102 (in part).

Diagnosis: Large, with subglobose to broadly conical shell. Female bursa copulatrix pyriform, with medium length duct.

Type locality: Green River, Wyoming (not subsequently restricted). Holotype, USNM 526631.

Remarks: *Fluminicola coloradensis* is the large, globose-shelled species with a prominent adapical shoulder and thickened lip that lives in large springs and streams in the Green River and Bonneville basins. This snail was typically referred to as *F. fusca* or *F. hindsii* in the early literature, but in a recent review of the genus (Hershler & Frest, 1996), *F. coloradensis* was shown to be distinct from *F. fusca* (junior synonym, *Ammicola hindsii* Baird, 1863), which lives in the lower Snake River and Columbia River basins. Hershler & Frest (1996) conservatively attributed *F. coloradensis* solely to the Green River basin, but additional study has shown that Bonneville basin material conforms to this species (e.g., Figure 8A, B) as earlier suggested by Morrison (1940:125). Variation among populations of *F. coloradensis* generally is minor, involving slight differences in shell shape, development of an adapical shoulder on teleoconch whorls, thickness of the inner lip, and penis size. Although a few populations closely similar to *F. coloradensis* are found in the middle portion of the Snake River basin (e.g., Little Wood River), confident confirmation of conspecificity of these with *F. coloradensis* is beyond the scope of this study. Material from springs in Malad Valley (in the northeast segment of the Bonneville basin), and adjacent portions of the Snake River basin (Arbon Valley, Portneuf River drainage) have a distinctively purple shell, and a higher spire and thinner lip than in characteristic *F. coloradensis* (Figure 8C). Anatomically this snail is entirely consistent with *F. coloradensis*, and historical samples of shells from the Malad River also closely conform to typical *F. coloradensis*. Although I treat the Malad Valley material herein as *F. coloradensis*, this problem merits further study. Chamberlin & Jones (1929) suggested that a second species of *Fluminicola* (identified by them as *F. seminalis*) lives in Utah, but material that I have seen from the localities that they referenced (Utah Lake, Tooele Valley) conforms to *F. coloradensis*.

Material examined: IDAHO. Bear Lake County: Bear Lake, Fish Haven, USNM 715883 (subfossil).—Caribou County: Bear River, Soda Springs, USNM 526730.—Kackley Spring, Gem Valley, T. 10 S, R. 40 E, SW ¼ section 21, USNM 883540, USNM 883700, USNM 883890.—spring, southeast of Kackley Spring, Gem Valley, T. 10 S, R. 40 E, NW ¼ section 27, USNM 883698. Oneida County: Big Malad Spring, USNM 883479, USNM 883892.—Little Malad Spring, Malad Valley, T. 12 S, R. 34 E, SW ¼ section 14, USNM 883391, USNM

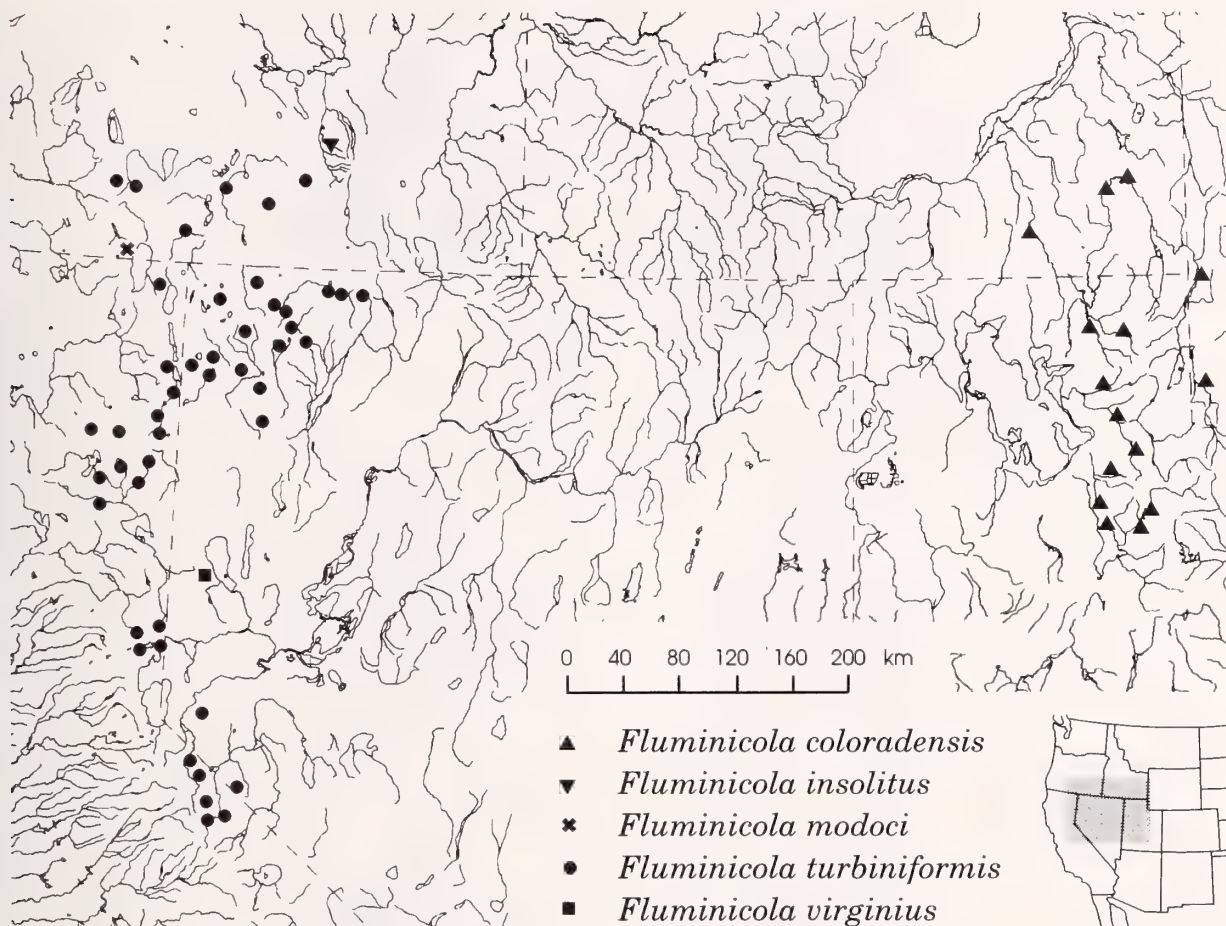
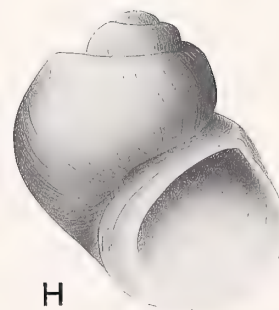
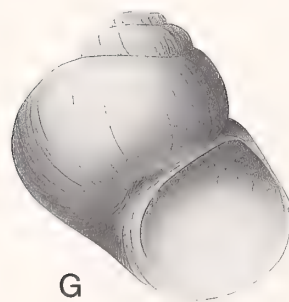
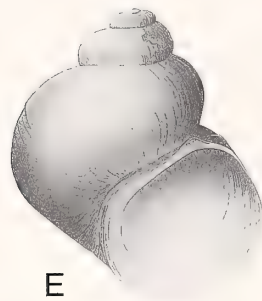
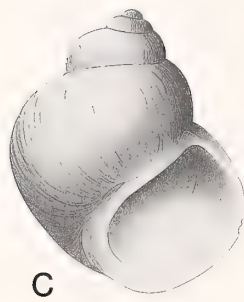
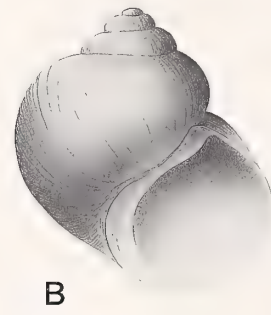
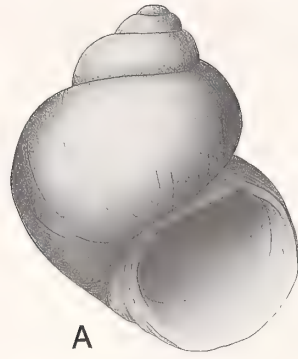


Figure 7

Map of northern Great Basin and adjacent regions showing the distribution of *Fluminicola* species. The type locality of *F. modoci* and previously reported localities for *F. coloradensis* in the Green River drainage (see Hershler & Frest, 1996) are not shown.

883887. **UTAH.** *Elder County:* Malad River, ANSP 62606, FMNH 224425, USNM 47873. *Cache County:* Blacksmith Fork, below Ballard Springs, Cache Valley, FMNH 178420.—Blacksmith Fork, Cache Valley, T. 10 N, R. 2 E, NE ¼ section 9, USNM 883855, USNM 883861.—Murray Spring, Cache Valley, T. 10 N, R. 1 W, SE ¼ section 9, USNM 883475, USNM 883863. *Morgan County:* East Canyon Creek, Weber River drainage, T. 2 N, R. 3 E, NW ¼ section 35, USNM 883854, USNM 883858.—Weber River, HWY 84, south of Peterson, T. 4 N, R. 2 E, NE ¼ section 6, USNM 874068, USNM 883280, USNM 883862. *Rich County:* Bear Lake, west shore, FMNH 179555.—Bear Lake, FMNH 178364.—Bear Lake, east shore, FMNH 178365. *Salt Lake County:* Salt Lake City, USNM 519988.—spring, south of Riverton, Jordan River drainage, T. 4 S, R. 1 W, NW ¼ section 5, USNM 883241, USNM 883286, USNM 883859. *Tooele County:* Tooele Valley, FMNH 178414.—Cotton-

wood Creek, Holladay, Jordan River drainage, FMNH 178361. *Utah County:* Spring Creek, Utah Lake drainage, T. 5 S, R. 1 E, SW ¼ section 15, USNM 883242, USNM 883860.—Utah Lake, ANSP 27772, ANSP 365332, FMNH 224328, FMNH 224330, USNM 9222, USNM 75452, USNM 31270.—Utah Lake, west shore, FMNH 178857.—Utah Lake, near Saratoga, FMNH 178394, FMNH 179556.—Provo Canyon, above Vivian Park, Utah Lake drainage, FMNH 178355, FMNH 178367. *Wasatch County:* Provo River, below Charleston, FMNH 179221, FMNH 179222. *Weber County:* 0.8 km below Ogden Canyon, FMNH 178391.—just outside Ogden Canyon, Ogden, ANSP 144614.—entrance to Ogden Canyon, Ogden, ANSP 145845.—Ogden River, FMNH 178396. **WYOMING.** Green River, USNM 526631. *Lincoln County:* Smiths Fork, Bear River drainage, T. 24 N, R. 119 W, NE ¼ section 5, USNM 883902. *Uinta County:* Bear River, HWY 89, northwest of Evanston, T. 16 N, R.



121 W, NW $\frac{1}{4}$ section 13, USNM 883525, USNM 883864, USNM 883865.

Fluminicola insolitus, Hershler, sp. nov.

Donner und Blitzen pebblesnail

(Figures 7, 8D, 9, 10A–C)

Lithoglyphus turbiniformis (Tryon, 1865), Taylor, 1966a, fig. 9 (in part).—Taylor, 1985:309 (in part; "headwaters of the Donner und Blitzen River").

Etymology: From New Latin *insolitus*, meaning unusual or uncommon, and referring to the divergent aspect of this species.

Diagnosis: Medium-sized with trochoidal shell. Female bursa copulatrix ovate, with medium length duct.

Description: Shell (Figure 9A) trochoidal, rarely with eroded spire; height, 3.6–4.2 mm; whorls, 3.75–4.0. Protoconch (Figure 9B) of 1.5 whorls, diameter about 0.76 mm; microsculpture of numerous weak spiral striae. Teleoconch whorls convex, usually evenly rounded, rarely shouldered. Microsculpture of well-developed collabral growth lines and weak, often eroded, spiral striae. Periostracum olive. Shell opaque, dark gray or purple. Aperture large, lunate, weakly angled adapically. Outer lip prosocline, thin. Parietal lip thin, complete across body whorl, adnate. Columellar swelling broad, covering near entirety of umbilical region. Shell usually anomphalous, rarely narrowly umbilicate.

Operculum (Figure 9C, D) thin, light amber, ovate, paucispiral; outer margin without rim. Attachment scar margin slightly thickened all around. Callus weakly developed.

Radula with about 80 rows of teeth; ribbon length, 2.4 mm, ribbon width, 160 μ m; central tooth width, 62 μ m. Cutting edge of central tooth (Figure 9E, F) weakly indented; lateral cusps, 3–6; median cusp narrow U-shaped, slightly broader and longer than laterals; basal cusps absent; basal tongue broad, extending below lateral margins, basal sockets weakly excavated. Lateral margins angled about 50° relative to vertical axis of teeth; margins narrow, thin. Lateral tooth (Figure 9G) with slightly convex cutting edge. Lateral wing 60% of length of cutting edge; tooth face broader than tall; central cusp U-shaped, lateral cusps, 3–5 (inner), 4–6 (outer). Inner marginal teeth (Figure 9H) with 16–19 cusps; outer marginal teeth (Figure

9I) with 13–23 cusps. Cusps on inner marginal teeth larger than those on outer marginals. Salivary glands long, unpigmented. Stomach longer than style sac.

Snout, tentacles, foot dark brown or black. Bases of tentacles around eyes sometimes pale. Neck light gray. Pallial roof and visceral coil dark brown or black, pigment somewhat lighter on gonads and genital ducts; pallial edge black.

Ctenidium positioned slightly anterior to pericardium; filaments about 21, small, taller than wide, without pleats. Osphradium about 33% of ctenidium length. Hypobranchial gland without anterior swelling. Renal organ with prominent (45%) pallial portion; renal opening simple. Cephalo-pedal ganglia weakly pigmented.

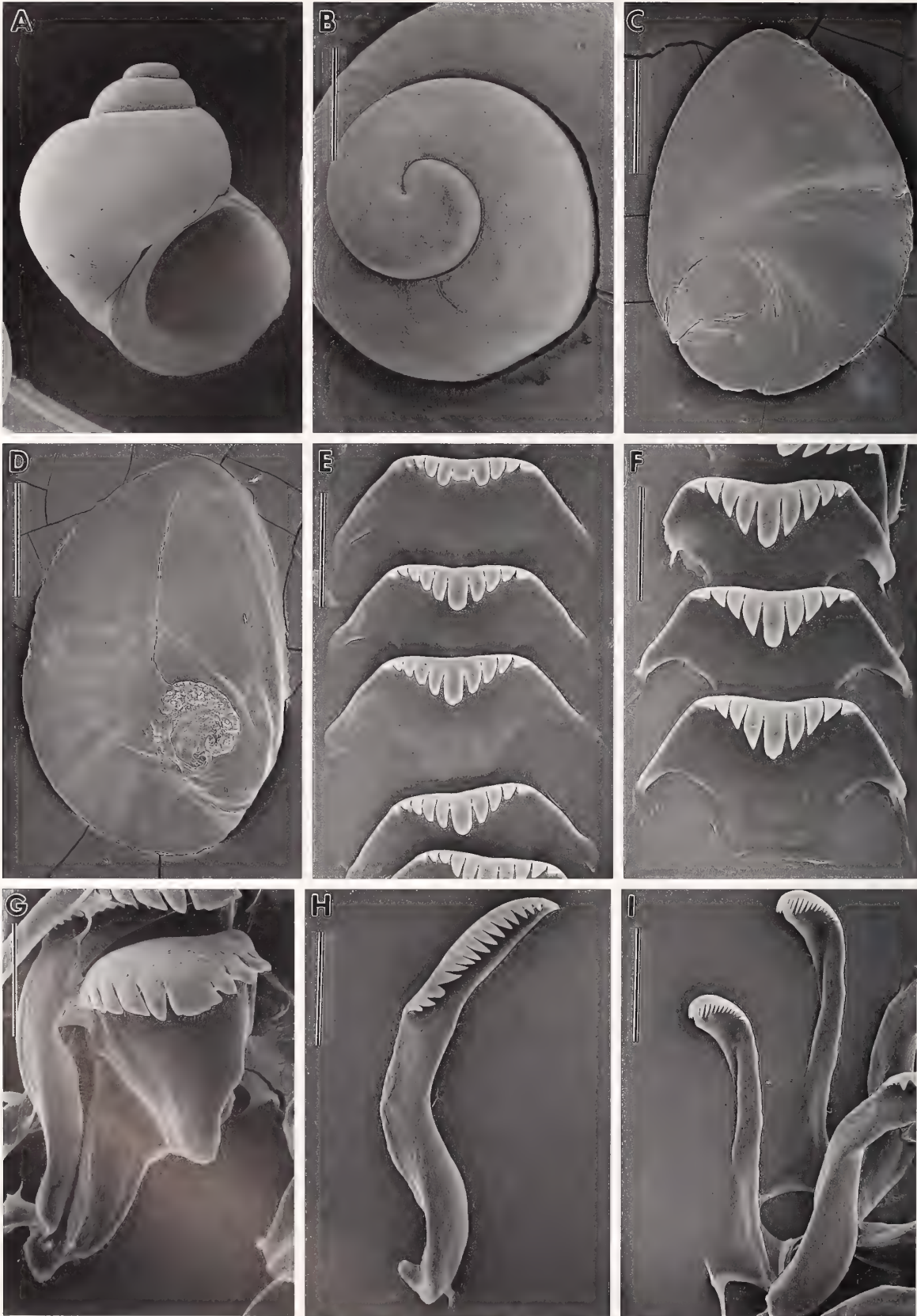
Ovary 0.25–0.5 whorl, abutting or slightly posterior to edge of stomach, filling less than 50% of digestive gland behind stomach. Distal female genitalia shown in Figure 10A, B. Coiled oviduct posterior-oblique; proximal arm strongly kinked or with small coil; distal arm swollen with sperm. Coiled oviduct and bursal duct join just behind pallial wall (slightly behind posterior edge of capsule gland). Bursa copulatrix about 60% of albumen gland length; ovate, transversely oriented, about 50% overlapped by albumen gland. Bursal duct medium length (ca. 50% of bursa length), narrow, originating near ventral edge of bursa copulatrix. Seminal receptacle much smaller than bursa copulatrix, positioned just anterior to bursa copulatrix along posterior edge of albumen gland, completely overlapped by albumen gland. Albumen gland with deep rectal furrow; furrow weakly developed on capsule gland. Albumen gland without pallial component; capsule gland with short visceral section. Capsule gland about as long as, but narrow than albumen gland; capsule gland folded over to the right. Ventral channel without anterior vestibule. Genital opening a small terminal slit.

Testis 1.0–1.25 whorl, overlapping posterior stomach chamber, filling more than 50% of digestive gland length behind stomach. Prostate gland with 33% of length in pallial roof. Pallial vas deferens with weak proximal kink; portion of vas deferens in neck straight. Penis (Figure 10C) medium to large, broad sickle shape, curved, without folds; base sometimes slightly narrowed, medial section without taper; distal section rounded, with short, narrow papillalike tip. Penial duct near central, undulating throughout (more pronounced distally). Penis pale or with light dusting of melanin proximally.

←

Figure 8

Type and other shell material for Great Basin species of *Fluminicola*. A. *F. coloradensis*, ANSP 27772 (shell height 8.1 mm). B. *F. coloradensis*, USNM 883280 (8.5 mm). C. *F. coloradensis*, USNM 883479 (8.5 mm). D. *F. insolitus* Hershler, sp. nov., holotype, USNM 883466 (3.7 mm). E. *F. turbiniformis*, USNM 858249 (4.8 mm). F. *F. turbiniformis*, USNM 883527 (2.0 mm). G. *F. turbiniformis*, USNM 858241 (3.2 mm). H. *F. virginus* Hershler, sp. nov., holotype, USNM 874902 (2.7 mm).



Type locality: Page Springs, Donner und Blitzen River drainage, Harney County, Oregon, T. 32 S, R. 32½ E, NW ¼ section 17. A small rheocrene (11°C, 89 micromhos/cm) draining west to the Donner und Blitzen River (Figure 4C). This site did not appear disturbed when visited in 1993. Holotype, USNM 883466 (Figure 8D), collected by D. W. Sada, 8 July 1993; paratypes, USNM 860757.

Remarks: This snail, endemic to the type locality (Figure 7), is unique in the genus in having a very broad basal process of the central radular teeth and lacking basal cusps on these teeth. *Fluminicola insolitus* most closely resembles *F. turbiniformis*, which also lives in the north-west Great Basin (see below) and with which it was previously confused (Taylor, 1966a, 1985), but further differs from this species in the purple tint of its shell, thinner shell parietal lip, stouter lateral radular teeth, and stouter bursa copulatrix with longer duct.

Material examined: OREGON. *Harney County:* Page Springs, Donner und Blitzen River drainage, USNM 860757, USNM 883192, USNM 883466.

Fluminicola modoci Hannibal, 1912

(Figure 7)

Fluminicola modoci Hannibal, 1912:187, pl. 8: fig. 30.—Turgeon et al., 1988:60.—Hershler & Frest, 1996:13–14, figs. 4F, 5H–J, 6E, 7D, 8J–L, 9D, 10D, 11.

Lithoglyphus modoci (Hannibal, 1912), Taylor, 1975:125 (literature compilation).

Diagnosis: Small with broadly conical shell. Female bursa copulatrix sub-globose, with short duct.

Type locality: Fletchers Spring, south end, Goose Lake, California. Lectotype, CAS 60798.

Remarks: Hershler & Frest (1996) discussed problems with the types and identity of this species. Dry Creek discharges into the northwestern side of Goose Lake (Figure 7) about 32 km north of the type locality area. Snails from the Dry Creek spring have broad, typically decollate shells closely conforming to *F. modoci*.

Material examined: CALIFORNIA. *Modoc County:* Fletchers Spring, south end, Goose Lake, CAS 60798. OREGON. *Lake County:* spring, source of Dry Creek, Goose Lake basin, T. 40 S, R. 17 E, SE ¼ section 36, USNM 883554, USNM 883558.

Fluminicola turbiniformis (Tryon, 1865)

(Figures 7, 8E–G)

Amnicola turbiniformis Tryon, 1865:219, pl. 22: fig. 5.

Fluminicola turbiniformis (Tryon, 1865), Baker, 1964: 177.—Turgeon et al., 1988:61.—Hershler & Frest, 1996:16–17, figs. 5K, L, 6H, 9F, 13D, 14, 16B, 17D–F, 18B.

Lithoglyphus turbiniformis (Tryon, 1865), Taylor, 1966a:24, fig. 9 (in part).—Taylor, 1975:197 (in part; literature compilation).—Taylor, 1985:309 (in part).

Diagnosis: Small with ovate to narrow-conic shell. Female bursa copulatrix ovate, with short duct.

Type locality: west side of Steens Mountain, Catlow Valley, Oregon. The type locality has not been precisely located. Lectotype, ANSP 27779.

Remarks: This species ranges widely throughout the northwest Great Basin, from Lake Abert basin east to Quinn River basin and south to Walker River basin (Figure 7). This range conforms in part to that depicted by Taylor (1966a:fig. 9), although populations in the Donner und Blitzen River drainage and the eastern side of the Pyramid Lake basin are herein described as new species, and I do not recognize *F. turbiniformis* in the Sacramento and Columbia River basins. I am also unable to confirm presence of *F. turbiniformis* in the Deschutes River drainage as reported by Taylor (1985:309). Populations of *F. turbiniformis* vary in size, relative shell height, width of columellar lip, and excavation of umbilical region (Figure 8E–G); and also in size of penis relative to head. Several populations in the Smoke Creek Desert and Honey Lake basin in northeast California are distinguished by their especially large size, rather globose, frequently decollate shell with thin shell lip (Figure 8G), but intergradation with more typical *F. turbiniformis* is apparent.

Material examined: CALIFORNIA. *Alpine County:* spring, Monitor Creek, Carson River basin, T. 9 N, R. 21 E, section 3, USNM 854752.—springs, northeast side of Bagley Valley, Carson River basin, T. 9 N, R. 21 E, NE ¼ section 15, USNM 858240. *Lassen County:* spring, Old Marr Ranch, Duck Flat, T. 37 N, R. 17 E, NE ¼ section 31, USNM 858252.—springs, west of Dairy Spring, Grasshopper Valley, T. 34 N, R. 11 E, SW ¼ section 4, USNM 858248.—spring, Painters Creek, Madeline Plains, T. 34 N, R. 17 E, NW ¼ section 30, USNM 858250.—springs, Cold Spring Valley, Madeline Plains,

Figure 9

Scanning electron micrographs of shell, operculum, and radula of *Fluminicola insolitus* Hershler, sp. nov., USNM 860757. A. Shell (height 3.5 mm). B. Shell apex. Bar = 300 µm. C. Operculum, outer surface. Bar = 428 µm. D. Operculum, inner surface. Bar = 444 µm. E, F. Central radular teeth. Bars = 26 µm. G. Lateral radular tooth. Bar = 20.5 µm. H. Inner marginal tooth. Bar = 23 µm. I. Outer marginal teeth. Bar = 26 µm.

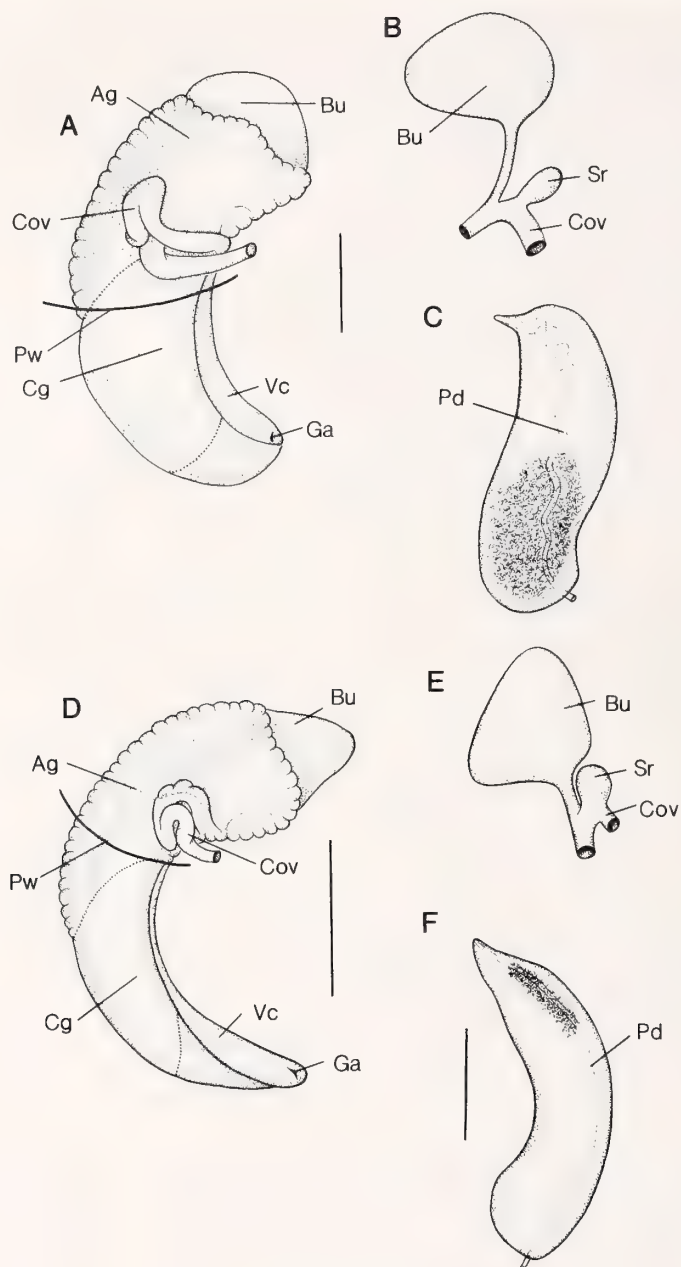


Figure 10

Genitalia of *Fluminicola* species (A–C, *F. insolitus* Hershler, sp. nov., USNM 860757; D–F, *F. virginius* Hershler, sp. nov., USNM 874103). A. Left side of female glandular oviduct and associated structures. Bar = 0.5 mm. B. Bursa copulatrix and seminal receptacle. Scale as in “A.” C. Dorsal surface of penis. Scale as in “A.” D. Left side of female glandular oviduct and associated structures. Bar = 0.5 mm. E. Bursa copulatrix and seminal receptacle. Scale as in “D.” F. Dorsal surface of penis. Bar = 0.25 mm. Ag, albumen gland; Bu, bursa copulatrix; Cg, capsule gland; Cov, coiled oviduct; Ga, genital aperture; Pd, penial duct; Pw, posterior wall of pallial cavity; Sr, seminal receptacle; Vc, ventral channel of capsule gland.

T. 36 N, R. 16 E, SW $\frac{1}{4}$ section 18, USNM 858251.—Bailey Creek, Madeline Plains, T. 34 N, R. 12 E, NE $\frac{1}{4}$ section 15, USNM 858249.—spring, south of HWY 36 ca. 4.8 km west of Susanville, Susan River basin, T. 30 N, R. 11 E, SW $\frac{1}{4}$ section 35, USNM 858244.—Five Springs, Honey Lake basin, T. 31 N, R. 16 E, NE $\frac{1}{4}$ section 23, USNM 858247.—spring, Willow Creek, Willow Creek Valley, T. 32 N, R. 11 E, SE $\frac{1}{4}$ section 35, USNM 874933.—Shoals Creek, Horse Lake basin, T. 32 N, R. 13 E, NW $\frac{1}{4}$ section 6, USNM 858245, USNM 858246.—Tule Patch Spring, Honey Lake basin, T. 32 N, R. 15 E, SE $\frac{1}{4}$ section 10, USNM 854468, USNM 858256, USNM 873394.—spring, east of Sage Hen Spring, Smoke Creek, T. 33 N, R. 16 E, SW $\frac{1}{4}$ section 25, USNM 874054.—springs, Shinn Ranch, Smoke Creek, T. 33 N, R. 16 E, SW $\frac{1}{4}$ section 36, USNM 858257, USNM 874100.—Big Spring, Smoke Creek, T. 33 N, R. 16 E, NW $\frac{1}{4}$ section 3, USNM 858260, USNM 858338.—spring, southwest of Sage Hen Spring, Smoke Creek, T. 33 N, R. 16 E, NE $\frac{1}{4}$ section 35, USNM 858258.—Sage Hen Spring, Smoke Creek, T. 33 N, R. 16 E, NE $\frac{1}{4}$ section 35, USNM 858259. *Modoc County*: springs, 1.1 km north of Fandanga Pass turnoff, Surprise Valley, T. 46 N, R. 16 E, NE $\frac{1}{4}$ section 31, USNM 858255.—Von Ripper Spring, Surprise Valley, T. 39 N, R. 16 E, NW $\frac{1}{4}$ section 25, USNM 858253.—spring, southwest of Von Ripper Spring, Surprise Valley, T. 39 N, R. 16 E, NW $\frac{1}{4}$ section 36, USNM 858254. *Mono County*: spring, Silver Creek, Pickel Meadow, West Walker River basin, T. 6 N, R. 22 E, NW $\frac{1}{4}$ section 24, USNM 873406.—springs, east side West Walker River, T. 6 N, R. 23 E, NE $\frac{1}{4}$ section 9, USNM 873361.—springs, west side Little Walker River, T. 6 N, R. 23 E, SW $\frac{1}{4}$ section 15, USNM 873412.—springs, southeast corner Slinkard Valley, West Walker River basin, T. 8 N, R. 22 E, SW $\frac{1}{4}$ section 15, USNM 873346. *Nevada County*: spring, Sagehen Creek, Little Truckee River basin, T. 18 N, R. 15 E, section 1, USNM 892040.—spring, Sagehen Creek, Little Truckee River basin, T. 18 N, R. 15 E, section 3, USNM 892042.—spring, Sagehen Creek, Little Truckee River basin, T. 18 N, R. 16 E, section 6, USNM 892041.—Boca Spring, Truckee River basin, T. 18 N, R. 17 E, NE $\frac{1}{4}$ section 10, USNM 858242. *Sierra County*: spring, east side HWY 89, south of Kyburz Flat, Little Truckee River basin, T. 19 N, R. 16 E, NW $\frac{1}{4}$ section 29, USNM 858241.—spring, Hoke Valley, Little Truckee River basin, T. 19 N, R. 17 E, SW $\frac{1}{4}$ section 2, USNM 858243, USNM 858357. *NEVADA. Humboldt County*: North Hell Creek Spring, Virgin Valley, T. 44 N, R. 24 E, NW $\frac{1}{4}$ section 3, USNM 873213, USNM 873226, USNM 874218.—Boulder Spring, Virgin Valley, T. 44 N, R. 25 E, SW $\frac{1}{4}$ section 19, USNM 874049.—The Dip (spring), Hell Creek, Virgin Valley, T. 44 N, R. 24 E, SW $\frac{1}{4}$ section 9, USNM 873207.—spring, Cherry Gulch, Bog Hot Valley, T. 45 N, R. 29 E, SW $\frac{1}{4}$ section 8, USNM 883933.—spring, Fivemile Flat, Summit Lake basin, T. 43 N, R. 25

E, SE $\frac{1}{4}$ section 35, USNM 892030.—spring, Antelope Creek, T. 46 N, R. 30 E, NW $\frac{1}{4}$ section 28, USNM 874212.—Antelope Springs, Soldier Meadow, T. 41 N, R. 25 E, NW $\frac{1}{4}$ section 32, USNM 883526.—spring, Bartlett Creek, Black Rock Desert, T. 41 N, R. 27 E, SE $\frac{1}{4}$ section 5, USNM 883901.—spring, Virgin Creek, Quinn River Valley, T. 46 N, R. 30 E, NE $\frac{1}{4}$ section 34, USNM 874213, USNM 874738. *Lyon County*: spring, upper Illinois Canyon, Carson River basin, T. 14 N, R. 22 E, SE $\frac{1}{4}$ section 7, USNM 874903, USNM 883527.—spring, Sweetwater Mountains, West Walker River basin, T. 8 N, R. 24 E, SE $\frac{1}{4}$ section 27, USNM 854627 (southern spring), USNM 854628 (middle spring). *Washoe County*: spring, South Catnip Creek, Guano Valley, T. 46 N, R. 22 E, NE $\frac{1}{4}$ section 24, USNM 874206.—spring, Wall Creek, 4.8 km above reservoir, Duck Flat, T. 38 N, R. 20 E, NE $\frac{1}{4}$ section 6, USNM 854706.—spring, northeast of Middle Lake, Long Valley, T. 46 N, R. 21 E, center section 30, USNM 854753.—spring, near southeast corner of Boulder Reservoir, Boulder Flat, T. 40 N, R. 20 E, NE $\frac{1}{4}$ section 32, USNM 874186.—spring, east side of Hays Canyon Range, Boulder Flat, T. 40 N, R. 19 E, SW $\frac{1}{4}$ section 32, USNM 874266.—spring, south of Garden Lake, Duck Flat, T. 35 N, R. 18 E, SW $\frac{1}{4}$ section 12, USNM 883927.—Clear Creek, Granite Mountain, Black Rock Desert, T. 34 N, R. 22 E, NE $\frac{1}{4}$ section 26, USNM 874290.—Clear Creek, Granite Mountain, T. 34 N, R. 22 E, section 26, USNM 854066.—spring (west of road), Bog Hog Ranch Creek, High Rock basin, T. 38 N, R. 23 E, NE $\frac{1}{4}$ section 19, USNM 874209.—spring (east of road), Bog Hog Ranch Creek, High Rock basin, T. 38 N, R. 23 E, NW $\frac{1}{4}$ section 20, USNM 874199.—spring, 3.2 km north-northwest of Little High Rock Reservoir, High Rock basin, T. 39 N, R. 23 E, NW $\frac{1}{4}$ section 30, USNM 874219.—Cottonwood Spring, High Rock basin, T. 43 N, R. 24 E, SE $\frac{1}{4}$ section 30, USNM 874215. *OREGON. Harney County*: west side of Steens Mountains, ANSP 27779.—Roaring Springs, Catlow Valley, T. 33 S, R. 30 E, NE $\frac{1}{4}$ section 31, USNM 883470.—Willow Spring, Catlow Valley, T. 36 S, R. 29 E, NW $\frac{1}{4}$ section 30, USNM 892029. *Lake County*: spring near source of Guano Creek, Guano Valley, USNM 883560.—spring, Dairy Creek, Chewaucan River drainage, T. 36 S, R. 17 E, SE $\frac{1}{4}$ section 12, USNM 883565.—spring, Dairy Creek, Chewaucan River drainage, T. 36 S, R. 17 E, SE $\frac{1}{4}$ section 11, USNM 883553.—Moss Spring, Lake Abert basin, T. 36 S, R. 19 E, SE $\frac{1}{4}$ section 5, USNM 883882.—springs, Deep Creek Falls, Warner Valley, T. 39 S, R. 23 E, NE $\frac{1}{4}$ section 23, USNM 883552.

Fluminicola virginius Hershler, sp. nov.

Virginia Mountains pebblesnail

(Figures 7, 8H, 10D–F, 11)

Lithoglyphus turbiniformis (Tryon, 1865), Taylor, 1966a, fig. 9 (in part).

Etymology: Referring to endemism of this snail in the Virginia Mountains west of Pyramid Lake.

Diagnosis: Medium-sized with trochoidal to low conic shell. Female bursa copulatrix ovate-pyriform, with short duct.

Description: Shell (Figure 11A) trochoidal to low conic, rarely with eroded spire; height, 2.9–3.4 mm; whorls, 3.25–3.75. Protoconch (Figure 11B, C) of 1.7 whorls, diameter about 0.50 mm; microsculpture of numerous spiral striae, often stronger close to periphery. Teleoconch whorls convex, often having peripheral angulation; shoulder well developed, often forming pronounced, rounded keel. Aperture and last 0.25–0.50 whorl disjunct. Microsculpture of well-developed collabral growth lines. Periostracum tan. Shell clear, translucent. Aperture large, ovate, angled above. Outer lip weakly prosocline, somewhat thickened. Parietal lip complete across body whorl, disjunct, thick. Columellar swelling broad; columellar lip thick. Shell anomphalous or narrowly umbilicate.

Operculum (Figure 11D, E) thin, light amber, ellipsoidal, paucispiral, nucleus highly eccentric; outer margin without rim. Attachment scar margin slightly thickened along inner edge. Callus weakly developed.

Radula with about 85 rows of teeth; ribbon length, 885 μm ; ribbon width, 115 μm ; central tooth width, 28 μm . Cutting edge of central tooth (Figure 11F) weakly indented; lateral cusps, 4–6; median cusp narrow U-shaped, pointed, slightly broader and longer than laterals; basal cusps, 1–2, cusp on outer side smaller; basal tongue V-shaped, even with lateral margins; basal sockets moderately excavated; lateral margins narrow, slightly thickened, angled about 55° to vertical axis of tooth. Cutting edge of lateral tooth (Figure 11G) horizontal or with weakly indented; cutting edge about 67% of length of lateral wing; tooth face taller than broad; central cusp rounded, narrow U-shaped, lateral cusps, 2–4 (inner), 3–5 (outer). Inner marginal teeth (Figure 11H) with 28–36 cusps; outer marginal teeth (Figure 11I) with 25–30 cusps. Cusps on inner marginal teeth larger than those on outer marginals. Stomach longer than style sac.

Snout light gray to black. Tentacles light gray to black, pigment often lighter around eyes. Foot light to medium gray. Opercular lobe black along inner edge. Pallial roof, visceral coil black.

Ctenidium positioned slightly anterior to pericardium; filaments about 14, small, about as tall as wide, without pleats. Osphradium about 38% of ctenidium length. Hypobranchial gland without anterior swelling. Renal organ with prominent (50%) pallial portion; renal opening slightly thickened. Cephalo-pedal ganglia pigmented.

Ovary 0.25–0.4 whorl, abutting or slightly overlapping edge of stomach, filling less than 50% of digestive gland behind stomach. Distal female genitalia shown in Figure 10D, E. Primary loop of coiled oviduct narrowly vertical to circular; distal arm swollen with sperm. Primary loop

preceded by smaller, narrowly vertical loop. Oviduct and bursal duct join behind pallial wall (slightly behind posterior edge of capsule gland). Bursa copulatrix about 55% of albumen gland length; ovate to pyriform, transversely oriented, about 50% overlapped by albumen gland. Bursal duct short (ca. 25–40% of bursa length), narrow, originating near ventral edge of bursa. Seminal receptacle smaller (33%) than bursa copulatrix, positioned slightly anterior or slightly overlapping bursa copulatrix near ventral edge of albumen gland, usually completely overlapped by albumen gland. Albumen gland with well-developed rectal furrow. Albumen gland with moderate (40%) pallial component; capsule gland entirely pallial. Capsule gland about as long, but narrower than albumen gland; capsule gland folded over to the right. Ventral channel without anterior vestibule. Genital opening a small terminal slit.

Testis 1.0 whorl, overlapping posterior stomach chamber, filling about 50% of digestive gland behind stomach. Prostate gland with 33% of length in pallial roof. Pallial vas deferens very narrow, straight; portion of vas deferens in neck straight. Penis (Figure 10F) medium-sized, sickle-shaped, weakly curved, without folds; base sometimes slightly narrowed, medium section without taper; distal section sharply pointed. Penial duct near outer edge, straight, surrounded by internal core of melanin distally. External surface of penis pale.

Type locality: Unnamed (“Waterfall”) spring, source of Hardscrabble Creek, Pyramid Lake basin, Washoe County, Nevada, T. 24 N, R. 20 E, SE $\frac{1}{4}$ section 13. A broad (400 m wide), shallow rheocrene (16.1°C, 144 micromhos/cm) (Figure 4D). Holotype, USNM 874902 (Figure 8H), collected by G. Vinyard, 31 October 1992; paratypes, USNM 860758.

Remarks: This species is distinguished from other congeners by the strongly (adapically) angled shell whorls, large shell aperture, and highly eccentric operculum nucleus. *Fluminicola virginius* otherwise closely resembles *F. turbiniformis*, although it also differs from this species in having a relatively longer bursal duct.

Material examined: NEVADA. Washoe County: Unnamed (“Waterfall”) spring, source of Hardscrabble Creek, Pyramid Lake basin, USNM 860758, USNM 874105, USNM 874902.

Pristinicola Hershler et al., 1994

Type species: *Bythinella hemphilli* Pilsbry, 1890; original designation.

Diagnosis: A monotypic northwestern United States genus having small to medium-sized, narrow-conic shell with wrinkled protoconch, smooth whorls, and simple aperture. Animal pale. Penis without accessory lobes or glands. Female coiled oviduct of tight loops; glandular

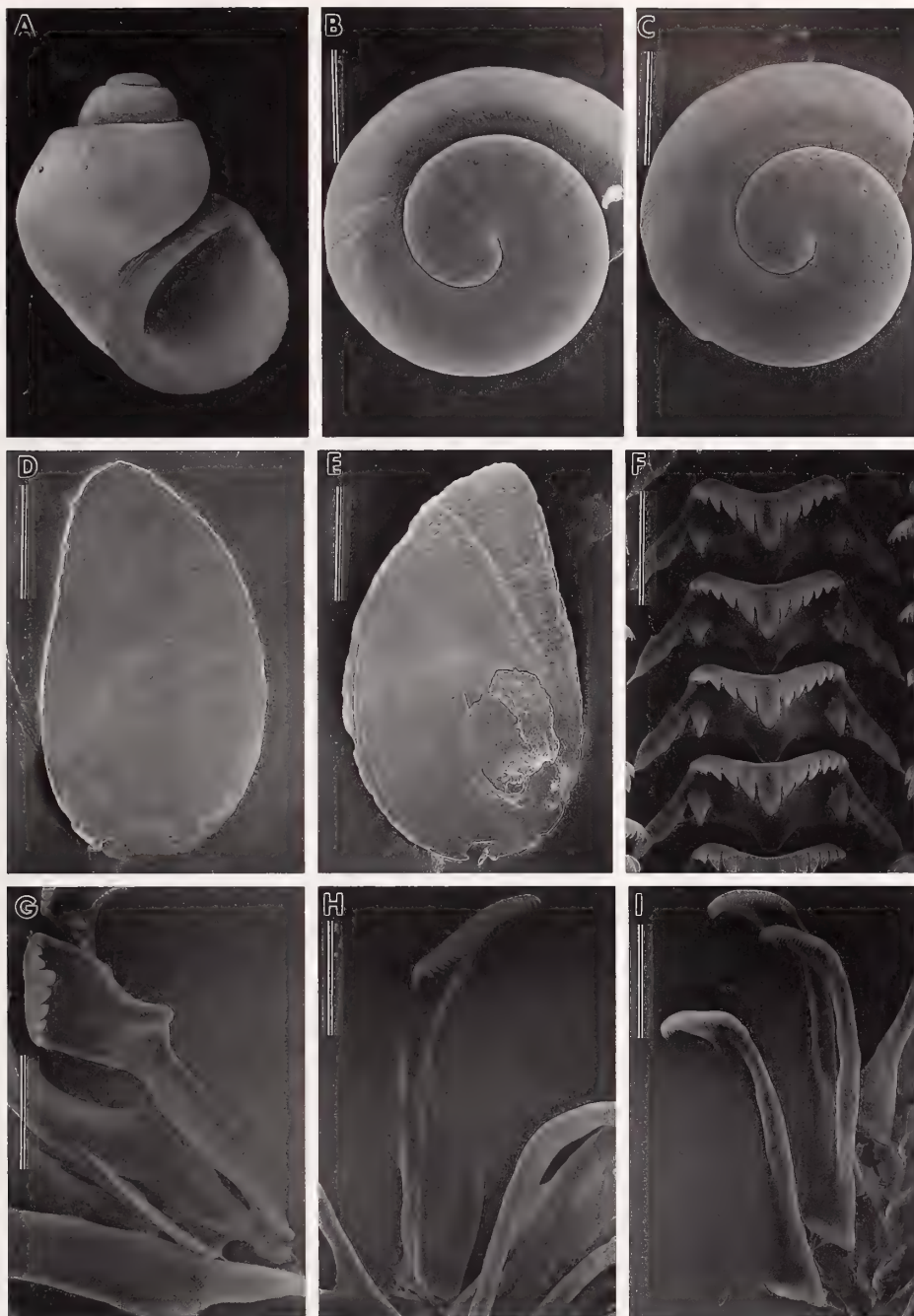


Figure 11

Scanning electron micrographs of shell, operculum, and radula of *Fluminicola virginius* Hershler, sp. nov. A. Shell, USNM 860758 (height 2.6 mm). B, C. Shell apex, USNM 860758. Bars = 300 μ m, 240 μ m, respectively. D. Operculum, outer surface, USNM 874105. Bar = 315 μ m. E. Operculum, inner surface, USNM 874105. Bar = 300 μ m. F. Central radular teeth, USNM 874105. Bar = 12 μ m. G. Lateral radular tooth, USNM 874105. Bar = 13.8 μ m. H. Inner marginal tooth, USNM 874105. Bar = 14.6 μ m. I. Outer marginal teeth, USNM 874105. Bar = 15 μ m.

oviduct large, ventrally closed; bursa copulatrix large, posteriorly recurved; seminal receptacle pouchlike.

Remarks: The single species in this genus was recently reviewed by Hershler et al. (1994).

Pristinicola hemphilli (Pilsbry, 1890)

(Figure 5)

Bythinella hemphilli Pilsbry, 1890:63.—Turgeon et al., 1988:60.

Pristinicola hemphilli (Pilsbry, 1890), Hershler et al., 1994: 225–233, figs. 1 (top row), 2–7.

Diagnosis: As for genus.

Type locality: Near Kentucky Ferry, Snake River, Washington. This locality has not been precisely located (Henderson, 1936; Hershler et al., 1994). Lectotype, ANSP 31176.

Remarks: The Great Basin populations closely resemble other material of this species, which previously was known from the lower Snake-Columbia River basin and other Pacific coastal drainages of Washington, with shells 3.0–3.5 mm tall and having about 5.0 whorls. The Great Basin localities (Figure 5) are upland waters which drain south to the Harney-Malheur basin. It is noteworthy that the fish faunas of the Great Basin and Columbia River drainage also overlap considerably in this region (Bisson & Bond, 1971).

Material examined: OREGON. *Harney County:* Mountain Spring, Silvies River drainage, T. 19 S, R. 32 E, SE $\frac{1}{4}$ section 3, USNM 883878.—Unnamed springs, Cricket Creek, Silvies River drainage, T. 21 S, R. 28 E, NW $\frac{1}{4}$ section 12, USNM 883875.—Adams Spring, head of Allison Creek, Silver Creek (Harney Lake drainage), T. 19 S, R. 26 E, SW $\frac{1}{4}$ section 12, USNM 883879. WASHINGTON. Near Kentucky Ferry, Snake River, ANSP 31176.

Eremopyrgus, Hershler, gen. nov.

Type species: *Eremopyrgus eganensis*, sp. nov.

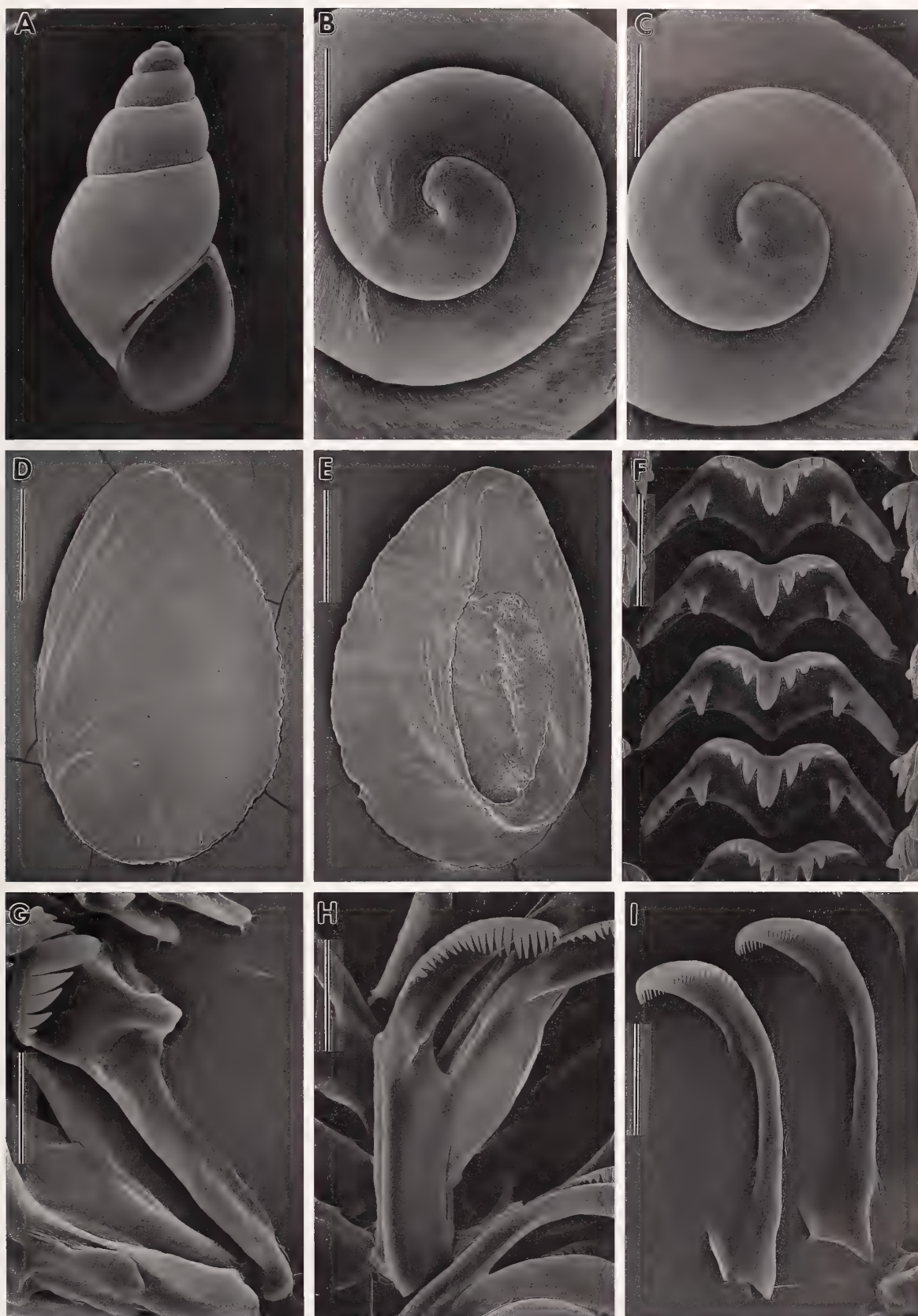
Etymology: From Greek, *eremos*, away from, separate; and *pyrgos*, tower. Referring to the isolation of this snail in eastern Nevada, and to its elongate shell. Gender masculine.

Diagnosis: A Great Basin cochliopine group having medium-sized, conical shell. Penis ornamented with two squat, glandular lobes, positioned along outer edge medially and inner edge distally. Distal portion of penis swollen, pointed, without terminal papilla. Females ovoviviparous; capsule gland thin-walled, functioning as brood pouch; bursa copulatrix large, seminal receptacle minute; fertilization duct coiled, opening to bursa copulatrix.

Description: Shell (Figure 12A) conical, with pronounced spire; height, 3.1–3.8 mm; whorls, 4.5–5.25, teleoconch whorls weakly convex, usually evenly rounded, sometimes having sub-sutural angulation. Shell clear-white, periostracum thin, brown. Protoconch (Figure 12B, C) of 1.60–1.75 whorls, diameter about 0.34 mm; initial portion often sculptured with a few, irregular wrinkles, later portion sometimes having a few weak spiral elements. Protoconch followed by distinct, relatively smooth 0.5 whorl corresponding to shell growth within the female brood pouch. Teleoconch microsculpture of faint growth lines and occasional weak spiral striae. Aperture medium-sized, narrowly ovate, strongly angled apically; outer lip rarely slightly thickened internally, orthocline or weakly prosocline, sometimes weakly sinuate; parietal lip complete across body whorl, thin, broadly adnate; columellar swelling absent or narrow. Shell anomphalous or rimate. Operculum (Figure 12D, E) medium thickness, amber, ellipsoidal, paucispiral, nucleus highly eccentric; outer margin without rim. Attachment scar margin thickened all around. Callus sometimes well developed. Salivary glands simple, narrow tubes. Radula with about 52 rows of teeth; ribbon length, 557 μm , ribbon width, 90 μm ; central tooth width, 22 μm . Central tooth (Figure 12F) with weak dorsal indentation; lateral cusps, 4–5; median cusp pointed, considerably broader and longer than laterals; basal cusp, 1; basal tongue V-shaped, often distinctly separated from remaining base, about even with lateral margins; basal sockets medium indented; lateral margins slightly thickened, inclined about 55° to vertical axis of teeth. Lateral tooth with slightly convex dorsal edge; lateral wings about 150% width of cutting edge; tooth face about as tall as wide; central cusp U-shaped; lateral cusps, 3–4 (inside), 4–5 (outside). Inner marginal teeth with 20–27 cusps; outer marginal teeth with 27–34 cusps. Cusps on inner marginals larger than those on out-

Figure 12

Scanning electron micrographs of shell, operculum, and radula of *Eremopyrgus eganensis* Hershler, sp. nov. A. Shell, USNM 860759 (height 3.3 mm). B, C. Shell apex, USNM 860759. Bars = 150 μm , 230 μm , respectively. D. Operculum, outer surface, USNM 883940. Bar = 333 μm . E. Operculum, inner surface, USNM 883940. Bar = 315 μm . F. Central radular teeth, USNM 883940. Bar = 10 μm . G. Lateral radular tooth, USNM 883940. Bar = 11 μm . H. Inner marginal tooth, USNM 883940. Bar = 11 μm . I. Outer marginal teeth, USNM 883940. Bar = 12 μm .



er marginals. Dorsal folds of esophagus long, straight. Cephalic tentacles medium length in preserved material. Tentacles pale or pigmented with scattered gray granules, sometimes forming longitudinal strip. Snout, foot pale or light to medium gray-brown. Opercular lobe sometimes black along inner edge. Neck pale or pigmented with scattered gray-brown granules. Pallial roof, visceral coil variably pigmented, usually light to medium brown, sometimes black. Ctenidium abutting pericardium; filaments about 22, well developed, slightly taller than wide, without pleats. Osphradium small (15%), centrally positioned. Hypobranchial gland well developed along rectum. Renal organ with large (50%) pallial portion; renal opening simple. Salivary glands small, tubular. Stomach longer than style sac, without posterior caecum. Cephalopodal ganglia strongly pigmented; cerebral, pedal commissures relatively long (ca. 50%). Oviduct terminating as narrow, blind tube just behind stomach. Distal female genitalia shown in Figure 13A, B. Coiled oviduct of a single, small posterior-oblique loop. Seminal receptacle a minute sac positioned along left side of bursa copulatrix near ventral edge. Seminal receptacle duct very short, opening to oviduct along ventral edge of bursa copulatrix just distal (and anterior) to oviduct coil (slightly behind the pallial wall) where also joined by the albumen gland and the narrow, coiled fertilization duct. Fertilization duct opening to left side of bursa copulatrix near anterior edge; duct having several tight coils on right side of bursa copulatrix before looping ventrally onto left side, where it coils once more before joining the oviduct. Bursa copulatrix relatively large, saclike, positioned along the left-ventral side of the brood pouch, extending to near the posterior edge of the brood pouch; duct short, narrow; sperm tube opening to pallial cavity a little anterior to pallial wall. Brood pouch large, posteriorly folded (and greatly narrowed) along right side of bursa copulatrix. Pouch containing relatively few (2–5) embryos having up to 2.5 whorls. Albumen gland very short, narrow, positioned along right edge of bursa copulatrix. Genital aperture a slightly muscularized terminal slit. Testis 1.0 whorl, overlapping posterior stomach chamber, filling about 50% of digestive gland behind stomach. Prostate gland strongly recurved, with about 50% of length in pallial roof. Anterior vas deferens exiting prostate gland a little behind anterior tip, in front of pallial wall. Pallial vas deferens narrow, with small posterior loop; portion of vas deferens in neck straight. Penis (Figure 13C) medium-sized, relatively narrow, weakly curved, gently tapering, inner edge somewhat swollen distally; penial tip pointed. Glandular penial lobes, 2, small, cuboidal, slightly expanded distally; glands filling distal half of lobes, discharging through rather large terminal openings. Lobe along inner edge distal, lobe along outer edge medial. Penial duct narrow, undulating throughout, positioned near outer edge. Penis pale except for small, dark area near tip.

Remarks: *Eremopyrgus* is assigned to the subfamily Cochliopinae (Hershler & Thompson, 1992) based on its specialized penial glands and female sperm tube separated from the glandular oviduct. This snail is distinguished from all other members of the subfamily by its unique glandular penial lobes, which bear some resemblance to those of members of the “*Heleobia* group” (Hershler & Thompson, 1992), but are cuboidal rather than spherical and do not have a large glandular lumen. *Eremopyrgus* further differs from the only member of the “*Heleobia* group” that broods young, *Mesobia* (locally endemic in Honduras), in having spiral (as opposed to wrinkled) protoconch sculpture, a distally pointed penis that lacks a terminal papilla, a much larger bursa copulatrix and much smaller seminal receptacle, much shorter ducts of both the bursa copulatrix and seminal receptacle, a more complexly coiled fertilization duct, and fewer brooded young. *Eremopyrgus* does not appear to be closely related to *Tryonia*, the only other member of the Cochliopinae reported from the Great Basin region.

Eremopyrgus eganensis Hershler, sp. nov.

Steptoe hydrobe
(Figures 3C, 12, 13A–C, 14)

Etymology: Refers to distribution of this species along the (eastern) flank of the Egan Range.

Diagnosis: As for genus.

Description: As for genus.

Type locality: spring, northwest of Clark Spring, Steptoe Valley, White Pine County, Nevada, T. 19 N, R. 63 E, NW ¼ section 20. A small rheocrene (19°C, 495 micromhos/cm) slightly disturbed by cattle (Figure 4E). Holotype, USNM 874692 (Figure 3C), collected by R. Hershler and P. Hovingh, 23 June 1992; paratypes, USNM 860759.

Remarks: *Eremopyrgus eganensis* lives in a group of small, closely proximate, warm springs in the southeast segment of Steptoe Valley (Figure 14).

Material examined: NEVADA. *White Pine County:* spring, northwest of Clark Spring, Steptoe Valley, USNM 860759, USNM 874692, USNM 883529, USNM 883940.—springs, Steptoe Ranch, T. 19 N, R. 63 E, SW ¼ section 5, USNM 873219.—“Big Spring,” Steptoe Ranch, T. 19 N, R. 63 E, SW ¼ section 5, USNM 873204.—spring, north of Steptoe Ranch, T. 19 N, R. 63 E, NE ¼ section 5, USNM 873209.

Tryonia Stimpson, 1865a

Type species: *Tryonia clathrata* Stimpson, 1865a; original designation.

Diagnosis: Minute to large, with elongate-conic to turri-

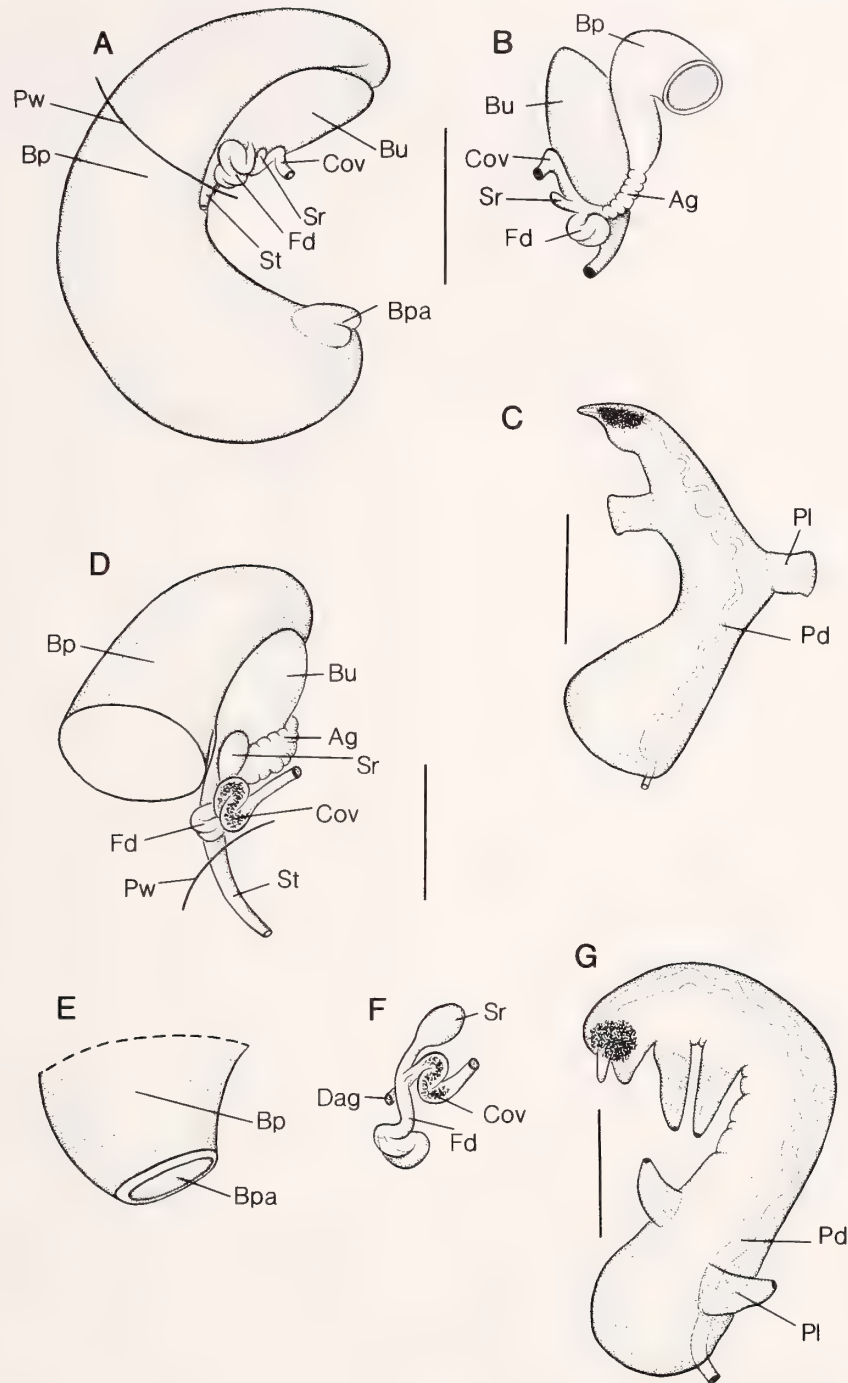


Figure 13

Genitalia of *Eremopyrgus* Hershler, sp. nov., and *Tryonia* species (A–C, *E. eganensis*; Hershler, gen. & sp. nov.; D–G, *T. monitorae*, Hershler, sp. nov. USNM 860760). A. Left side of female glandular oviduct and associated structures, USNM 883940. Bar = 0.5 mm. B. Right side of bursa copulatrix and associated structures, USNM 883940. Scale as in “A.” C. Dorsal surface of penis, USNM 874692. Bar = 0.25 mm. D. Left side of posterior portion of female glandular oviduct and associated structures. Bar = 0.125 mm. E. Left side of anterior portion of brood pouch, showing slightly muscularized opening. Scale as in “D.” F. Left side of seminal receptacle and associated structures (coiled oviduct rotated to left). Scale as in “D.” G. Dorsal surface of penis. Bar = 0.25 mm. Ag, albumen gland; Bp, brood pouch; Bpa, opening of brood pouch; Bu, bursa copulatrix; Cg, capsule gland; Cov, coiled oviduct; Fd, fertilization duct; Pd, penial duct; Pl, penial lobe; Pw, posterior wall of pallial cavity; Sr, seminal receptacle; St, sperm tube.



Figure 14

Map of the Great Basin (excluding northernmost portion) and adjacent regions showing the distribution of *Eremopyrgus* Hershler, gen. nov., and *Tryonia* species. The Mexican locality for *T. protea* is not shown.

form shell. Penis ornamented with one or more glandular papillae. Distal portion of penis having blunt, pigmented tip, a sub-terminal swelling along inner edge, and terminal papilla through which penial duct opens. Females ovoviviparous; capsule gland thin-walled, functioning as brood pouch; albumen gland highly reduced; bursa copulatrix and seminal receptacle small; fertilization duct coiled, opening to sperm tube.

Remarks: The scope and content of this genus remains poorly known as *Tryonia* has neither been subject to a modern revision nor been shown to be monophyletic. Many of the Recent species now allocated to the genus have not been well studied in terms of their anatomy. Taylor (1966b:196–198) placed numerous Recent-Tertiary high-spined species from North, Central, and South America into the genus, whereas Nuttall (1990:184–185) later questioned allocation of South American fossils to this group. Hershler & Thompson (1992) restricted the group to Pliocene-Recent species of North America.

Full descriptions of previously reported Great Basin species will be provided in a forthcoming review of this genus.

Tryonia clathrata (Stimpson, 1865a)

(Figure 14)

Tryonia clathrata Stimpson, 1865a:54, pl. 8, fig. 1.—Stimpson, 1865b:48–49, fig. 29.—Tryon, 1870:67.—Stearns, 1893:281.—Pilsbry, 1899:122.—Stearns, 1901:282.—Walker, 1918:139.—Gregg, 1941:118.—Baker, 1964:172.—Taylor, 1966b:197.—Taylor, 1975:58 (literature compilation).—Pratt, 1977:7.—Burch & Tottenham, 1980:100, fig. 134.—Williams et al., 1985:36, 45, 48.—Hershler & Thompson, 1987:figs. 1, 11, 12, 13–15, 19, 21–23.—Turgeon et al., 1988:63.—Hershler & Thompson, 1992:110, figs. 71a,c–e, 72.

Diagnosis: A medium to large species with turritiform shell; teleoconch sculpture of numerous, regularly spaced, collabral lamellae. Inner edge of penis ornamented with a single basal and four distal papillae.

Type locality: Given as “basin of the Colorado Desert,” but probably in error; subfossil. Lectotype, ANSP 27969. Stimpson (1865b:48) indicated that the type material was collected by Blake during his service on one of the Pacific Railroad Surveys. Stearns (1893) disputed the type locality as this species has not been found in numerous other samples from the Colorado Desert, whereas Merriam collected living specimens from Pahrnagat Valley (Nevada) well to the east. (Note that Pacific Railroad Survey expedition led by Lt. R. S. Williamson, with Blake serving as geologist, explored the Colorado Desert, but did not venture near southern Nevada [Blake, 1857].) Stearns (1901) later suggested that older Colorado Desert collections probably came from near Merriam’s locality. Morrison (1940) reiterated this point and suggested that early usage of the term “Colorado Desert” probably re-

ferred more generally to the Great Basin. Taylor (1966b) suggested that the type material probably came from the Muddy River (Moapa Valley, Nevada).

Baker (1964) designated ANSP 27969a as the lectotype. Although the original label associated with this lot merely identifies it as from Stimpson’s collection, with the locality, “Colorado Desert,” additional material from this lot, ANSP 30778, has a label identifying Blake as the collector, with the locality given as in Stimpson’s description.

Remarks: This species lives in warm springs in the White River trough (Moapa, Pahrnagat, White River Valleys) in southeastern Nevada (Figure 14). Extant populations conform to “Colorado Desert” material, with shells varying from about 2.9–7.0 mm, and having 5.75–8.75 whorls. Shell sculptural development varies from low, riblike ornament (rare) to well-developed, almost spinose lamellae. Whether or not *Tryonia clathrata spiralistriata* Wesselingh, 1996, from the Pliocene of Guatemala, is closely related to extant *Tryonia clathrata* is conjectural. As noted by Wesselingh (1996), these fossils, although similar to *T. clathrata* in size, shape and collabral shell sculpture, differ in having numerous well-developed spiral lirae on the teleoconch.

Material examined: Colorado Desert, ANSP 27969, USNM 27893, USNM 30596, USNM 56403, USNM 121072, USNM 170786. **NEVADA.** *Clark County:* 9.6 km northwest of Moapa, Moapa Valley, USNM 791488.—Muddy Spring, Moapa Valley, T. 14 S, R. 65 E, NE ¼ section 16, USNM 873358, USNM 873359.—Muddy Spring, 100 m below source, Moapa Valley, T. 14 S, R. 65 E, NE ¼ section 16, USNM 874346, USNM 874790.—springs, west of Muddy Spring, Moapa Valley, T. 14 S, R. 65 E, NW ¼ section 16, USNM 874351.—spring, west of Muddy Spring, Moapa Valley, T. 14 S, R. 65 E, NW ¼ section 16, USNM 874007, USNM 874024.—spring, 0.6 km south of above, Moapa Valley, T. 14 S, R. 65 E, NW ¼ section 16, USNM 850291, USNM 873192.—“Cardy Lamb Spring,” Moapa Valley, T. 14 S, R. 65 E, SW ¼ section 16, USNM 874352, USNM 874355, USNM 874788.—“Apcar Springs,” Moapa Valley, T. 14 S, R. 65 E, SE ¼ section 16, USNM 874349.—“Oasis Spring,” Moapa Valley, T. 14 S, R. 65 E, NW ¼ section 16, USNM 874010.—Moapa Valley Water District Spring, T. 14 S, R. 65 E, SE ¼ section 16, USNM 874018, USNM 874023.—spring, Moapa Valley National Wildlife Refuge, T. 14 S, R. 65 E, NE ¼ section 21, USNM 873356, USNM 873417, USNM 874343, USNM 874506, USNM 874787.—spring, 14.8 km northwest of Moapa, Moapa Valley, T. 14 S, R. 65 E, NE ¼ section 21, USNM 874080. *Lincoln County:* Pahrnagat Valley, USNM 123621.—warm spring, Pahrnagat Valley, USNM 107735. Ash Springs, Pahrnagat Valley, T. 6 S, R. 60 E, NE ¼ section 1, USNM 874011, USNM 874095, USNM 874789.—Crystal Spring, Pahrnagat

Valley, T. 5 S, R. 60 E, NE ¼ section 10, USNM 873157. *Nye County*: Hot Creek (source), White River Valley, T. 6 N, R. 61 E, NE ¼ section 18, USNM 873196, USNM 874306, USNM 874690.—Moorman Spring, White River Valley, T. 8 N, R. 61 E, SE ¼ section 32, USNM 873178.

Tryonia monitorae Hershler, sp. nov.

Monitor tryonia

(Figures 3D, 13D–G, 14, 15)

Etymology: Refers to endemism of this snail in Monitor Valley.

Diagnosis: A medium to large species with turritiform shell often weakly sculptured with spiral threads. Penis ornamented with single basal papillae along inner and outer edges, and two distal papillae along inner edge.

Description: Shell (Figure 15A) turritiform; height, 3.5–4.6 mm; whorls, 6.25–7.5. Apex flattened, often tilted; protoconch (Figure 15B) of 1.75 whorls, diameter about 0.41 mm; smooth. No obvious zone representing growth during brood period evident. Teleoconch whorls weakly to moderately convex, evenly rounded, without shoulders. Microsculpture of weak growth lines, sometimes strengthened at short intervals. Spiral threads often obvious on shells retaining periostracum; threads less obvious on cleaned shells. Periostracum brown. Shell clear. Aperture small, ovate. Outer lip thin, orthocline, often sinuate, with abapical portion advanced. Parietal lip often complete across body whorl, thin, broadly adnate. Columellar swelling absent. Shell anomphalous.

Operculum (Figure 15 C, D) thin, slightly convex, amber, ovate, paucispiral, whorls on outer surface weakly frilled; outer margin having weak rim. Attachment scar margin unthickened on inner surface. Callus absent.

Radula with about 47 rows of teeth; ribbon length, 400 µm, ribbon width, 75 µm; central tooth width, 19 µm. Central teeth (Figure 15 E, F) with moderate dorsal indentation; lateral cusps, 5–7; median cusp narrowly pointed, slightly broader and considerably longer than laterals; basal cusps, 1–2, inner cusp larger; basal tongue broad V-shaped, about even with lateral margins; basal sockets medium indented; lateral margins slightly thickened, strongly flared, often with distinct bend along outer edge, inclined about 50° to vertical axis of teeth. Lateral teeth

(Figure 15G) with very slight dorsal indentation; lateral wings slightly longer (120%) than width of cutting edge; tooth face slightly taller than wide; central cusp narrowly pointed; lateral cusps 3–4 (inside), 4–6 (outside). Inner marginal teeth (Figure 15H) with 19–25 cusps; outer marginal teeth (Figure 15I) with 18–27 cusps. Cusps on inner marginals larger than those on outer marginals.

Snout, tentacles, foot, neck unpigmented to medium gray-brown. Opercular lobe black along inner edge and sides. Pallial roof light gray to near black, visceral coil pale except for black pigment on stomach, to almost entirely black on all dorsal surfaces.

Ctenidium abutting pericardium; filaments about 35, well developed, about as tall as wide, pleated. Osphradium small (ca. 14%), positioned centrally or slightly posterior to middle of ctenidial axis. Hypobranchial gland not evident in dissection. Renal organ with moderate (30%) pallial bulge; renal opening slightly thickened. Salivary glands small, tubular. Stomach as long as style sac; anterior stomach chamber larger than posterior chamber. Cephalopedal ganglia unpigmented; cerebral commissure moderate length (ca. 43%); pedal commissure very short.

Oviduct terminating as slightly thickened tube a little behind stomach. Distal female genitalia shown in Figure 13 D–F. Coiled oviduct of two small, darkly pigmented overlapping loops (initial loop anterior-oblique, second loop posterior-oblique). Seminal receptacle a very small pouch just anterior to the bursa copulatrix (sometimes slightly overlapping left-dorsal surface). Seminal receptacle duct about as long as body, opening to coiled oviduct at point where latter connects with albumen gland. Fertilization duct of two small, tightly appressed coils opening to sperm tube (a little behind pallial wall) dorsal to coiled oviduct. Bursa copulatrix small, ovate, positioned along left-ventral side of brood pouch, extending to (or slightly posterior to) posterior edge of brood pouch, with narrow duct emerging from anterior edge; duct (to point where joined by fertilization duct) narrow, slightly longer than bursa copulatrix; sperm tube opening to pallial cavity a short distance in front of pallial wall. Brood pouch large, posteriorly folded along right side of bursa copulatrix. Pouch containing about 12 variably sized embryos; largest embryos of about 2.0 shell whorls. Albumen gland short, narrow, coursing ventrally across right side of bursa copulatrix and extending onto left side of bursa. Genital aperture broad, slightly muscularized.

Figure 15

Scanning electron micrographs of shell, operculum, and radula of *Tryonia monitorae* Hershler, sp. nov. A. Shell, USNM 860760 (height 2.6 mm). B. Shell apex, USNM 860760. Bar = 133 µm. C. Operculum, outer surface, USNM 883939. Bar = 200 µm. D. Operculum, inner surface, USNM 883939. Bar = 214 µm. E. Central radular teeth, USNM 883939. Bar = 10 µm. F. Central radular teeth, USNM 883941. Bar = 8.5 µm. G. Lateral radular tooth, USNM 883939. Bar = 10 µm. H. Inner marginal tooth, USNM 883939. Bar = 11 µm. I. Outer marginal teeth, USNM 883939. Bar = 10 µm.



Testis 1.5 whorl, occupying more than 50% of digestive gland behind stomach. Prostate gland small, ovate, with very short pallial component (13%). Anterior vas deferens exiting from anterior tip of prostate gland, slightly in front of pallial wall. Pallial vas deferens straight; portion of vas deferens in neck straight. Penis (Figure 13G) large, narrow, usually strongly curved, gently tapering, inner edge with pronounced bulge near terminus; penial tip rounded, with small terminal papilla. Glandular penial lobes, 4, small, conical. Basal lobes positioned on inner curvature and near outer edge. Distal lobes somewhat longer and narrower than basal lobes, positioned along inner curvature between middle of penis and distal bulge. Penial duct relatively broad, undulating except for distalmost section, positioned near outer edge. Penis pale or with light gray-brown external pigment; distal portion having small, prominent internal black patch near terminus.

Type locality: Hot Springs, Potts Ranch, Monitor Valley, Nye County, Nevada, T. 14 N, R. 47 E, NW ¼ section 1. Numerous hot springs are present in this area (Garside & Schilling, 1979:52). Snails were collected from a small thermal (34.5°C) rheocene (Figure 4F). Holotype, USNM 892046 (Figure 2D), collected by D. W. Sada, 4 August 1996; paratypes, USNM 860760.

Remarks: This snail is restricted to the type locality and the warm (31.5°) outflow of Dianas Punch Bowl (Figure 4G). These localities are located a few km apart (Figure 14) along a fault (Garside & Schilling, 1979:52, 53). This species closely resembles *T. margae* Hershler, 1989, from Death Valley, in shell shape and penial ornament, but is larger and also differs in having periostracal spiral sculpture, fewer opercular whorls, lighter body pigmentation, a narrower basal process on the central radular teeth, and smaller radular cusps. *Tryonia monitorae* differs from all other congeners that have been studied anatomically in that the albumen gland coils onto the left side of the bursa copulatrix.

Material examined: NEVADA. *Nye County:* Hot Springs, Potts Ranch, Monitor Valley, USNM 860760, USNM 874883, USNM 883530, USNM 883939, USNM 892046.—*Dianas Punch Bowl* (Hot Springs), Monitor Valley, T. 14 N, R. 47 E, SE ¼ section 22, USNM 874882, USNM 883941.

Tryonia protea (Gould, 1855)

(Figure 14)

Amnicola protea Gould, 1855:129–130.—Gould, 1857:332, pl. XI:figs. 6–9.—Johnson, 1964:132.

Melania exigua Conrad, 1855:269 (*non* Morelet, 1851).

Tryonia protea (Gould, 1855), Binney, 1865:71, 72, figs. 140–142.—Tryon, 1870:68.—Berry, 1948:59, 69.—Taylor, 1966a:53–54.—Taylor, 1966b:197.—Russell, 1971:232.—Taylor, 1975:160 (literature compila-

tion).—Burch & Tottenham, 1980:100, figs., 136, 137.—Taylor, 1981:153–154 (in part).—Taylor, 1985:317, fig. 35 (in part).—Turgeon et al., 1988:63.—Hershler, 1989:207–208, figs. 52–54.—Hershler & Thompson, 1992:111.

Bythinella protea (Gould, 1855), Stearns, 1893:278–281 (in part).

Paludestrina protea (Gould, 1855), Stearns, 1901:277–284, pl. XIX–XXI (in part).—Hannibal, 1912:186 (in part).—Walker, 1918:138–139 (in part).—Henderson, 1924:191, fig. 94.—Chamberlin & Jones, 1929:178.—Henderson, 1929:167, fig. 176.—Jones, 1940:44.

Hydrobia protea (Gould, 1855), Henderson, 1936:139.

Pyrgulopsis imminens Taylor, 1950:28, figs. 1–3.

Pyrgulopsis blakeana Taylor, 1950:30, figs. 4–6.

Pyrgulopsis cahuillarum Taylor, 1950:31–32, fig. 7.

Diagnosis: Large, narrowly turritiform, teleoconch often sculptured with spiral ridges and/or collabral ribs. Shell sculpture highly variable within and among populations, ranging from smooth to cancellate. Males unknown.

Type locality: Colorado Desert (Gran Jornada); subfossil. Syntypes, USNM 121074. Bequaert & Miller (1973:213) suggested that the type material probably came from Riverside County (California), near Salton View.

Remarks: Extant populations tend to have weaker sculpture than subfossil material from the type locality area. The species is disjunctly distributed, with populations concentrated in the upper Owens River drainage, lower Colorado River basin, Bonneville basin, and Lahontan basin (Figure 14). Taylor (1966a:53, 54) suggested that living populations assigned to this species may be composite, but I have not found this evident based on morphologic criteria. Late Pleistocene fossil records from Ivanpah Mountains and Pahrump Valley (Roth & Reynolds, 1990; Taylor, 1986, respectively) and live collections from Gila River drainage, Arizona (Bequaert & Miller, 1973:213) and Meadow Valley Wash, Nevada (Taylor, 1986:fig. 1) require confirmation. Gregg (1941) reported this species from Moapa, Nevada, but I suspect that his material represented relative smooth-shelled variants of *Tryonia clathrata*.

Material examined (exclusive of the numerous sub-fossil records from the type locality area): MEXICO. SONORA. spring, El Doctor, Colorado River drainage, USNM 873440, USNM 874183. CALIFORNIA. Colorado Desert, USNM 121074. *Mono County:* Hot Creek, Long Valley, T. 3 S, R. 28 E, NE ¼ sec. 25, USNM 857954, USNM 873362, USNM 874182, USNM 883309.—Whitmore Hot Springs, Long Valley, T. 4 S, R. 29 E, NE ¼ sec. 6, USNM 874180.—spring, tributary to Little Alkali Lake, Long Valley, T. 3 S, R. 29 E, NW ¼ section 29, USNM 873364, USNM 873365, USNM 874189. *Riverside County:* warm springs near Salton, USNM 104886.—Dos Palmas Spring, Salt Creek drainage, T. 8 S, R. 11 E, NW ¼ section 3, USNM 163227, USNM 791494.—spring, ca. 1.0 km WSW of Hunters

Spring, Salt Creek drainage, T. 8 S, R. 11 E, NE ¼ section 14, USNM 873367.—Hunters Spring, Salt Creek drainage, T. 8 S, R. 11 E, SW ¼ sec. 12, USNM 873443, USNM 874194, USNM 874469.—“Oasis Spring,” Salt Creek drainage, T. 8 S, R. 12 E, NE ¼ section 30, USNM 854744, USNM 873441, USNM 874196. NEVADA. *Clark County*: Blue Point Spring, Virgin River drainage, T. 18 S, R. 68 E, SW ¼ section 6, USNM 883248, USNM 883884. *Washoe County*: spring, tributary to Fly Reservoir, Hualapai Flat, T. 34 N, R. 23 E, SE ¼ section 2, USNM 892080. UTAH. *Juab County*: Percy Spring, Fish Springs Flat, T. 11 S, R. 14 W, SE ¼ section 26, USNM 854617, USNM 858283, USNM 883474.—South Springs, Fish Springs Flat, T. 11 S, R. 14 W, NE ¼ section 26, USNM 858286. *Tooele County*: Horseshoe Springs, Skull Valley, T. 2 S, R. 8 W, SE ¼ sec. 26, USNM 858291, USNM 883883.—first spring south of Josepha, Skull Valley, FMNH 178352, FMNH 224336.—spring at Josepha, Skull Valley, FMNH 178411.—spring before Josepha, Skull Valley, FMNH 178379.—Warm Springs, Tooele Valley, T. 2 S, R. 6 W, NE ¼ sec. 16.—spring, Blue Lake, Great Salt Lake Desert, T. 4 S, R. 19 N, NW ¼ sec. 7, USNM 883397.—Salt Spring, FMNH 178443, FMNH 224404.

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Land Caenogastropods of Mounts Mahermana, Ilapiry, and Vasiha, Southeastern Madagascar, with Conservation Statuses of 17 Species of *Boucardicus*

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Abstract. Quantitative, replicated altitudinal transects on the three mountains yielded 25 caenogastropod species in six genera in four families. *Madecataulus* Fischer-Piette & Bedoucha, 1965, is synonymized under *Boucardicus* Fischer-Piette & Bedoucha, 1965. Presence is noted of the three large species *Hainesia crocea* (Sowerby, 1847), *Tropidophora* sp. 1, and *T.* sp. 2. Descriptions are given of the small species *Boucardicus albocinctus* (E. A. Smith, 1893); *B. antiquus* sp. nov.; *B. carylae* sp. nov.; *B. culminans* (Fischer-Piette, Blanc, Blanc & Salvat, 1993); *B. curvifolius* sp. nov.; *B. delicatus* sp. nov.; *B. divei* Fischer-Piette, Blanc, Blanc & Salvat, 1993; *B. esetrae* sp. nov.; *B. fidimananai* sp. nov.; *B. fortistriatus* sp. nov.; *B. magnilobatus* sp. nov.; *B. mahermanae* sp. nov.; *B. rakotoarisoni* sp. nov.; *B. randalanai* sp. nov.; *B. simplex* sp. nov.; *B. tridentatus* sp. nov.; *B. victorhernandezi* Emberton, 1998; *Cyathopoma randalana* sp. nov.; *Malarinia calcopercula* Emberton, 1994; *Tropidophora (Ligatella) vallonzi* Fischer-Piette, Blanc, Blanc & Salvat, 1993; *Omphalotropis vohimenae* sp. nov.; and *O. costulata* sp. nov.

Distributional data were available that allowed evaluation of each of the 17 *Boucardicus* species for its conservation status, applying the latest IUCN criteria. Four species are proposed as Critically Endangered, 11 as Endangered, and two as Vulnerable.

INTRODUCTION

Recent quantitative sampling of altitudinal transects on Mounts Mahermana, Ilapiry, and Vasiha in southeastern Madagascar yielded 88 species of land snails and slugs (Emberton et al., 1996, 1999; Emberton, 1997). Of these, 81 species are small ("micro") land snails (< 5 mm in greatest dimension at any collected life stage). Analyses of the distributions of 80 of these species have shown that (a) the best sampling strategy for Madagascar-rain-forest snails is timed searching for micro-snails, while incidentally collecting macro-snails and litter-plus-soil for later picking of the 5.5–1.2 mm and the 1.2–0.85 mm, dry-sieved fractions (Emberton et al., 1996); (b) total land-snail diversity is significantly higher in the unprotected Vohimena Mountain Chain than in the protected Anosy Mountain Chain (Emberton et al., 1999); (c) the Vohimena Chain's greater richness occurs in four of the eight major groups of land snails (charopids; *Microcystis* Beck, 1837; *Kalidos* Gude, 1911; and non-*Boucardicus* "prosobranchs" [caenogastropods]), and does not exist for the other four groups (*Boucardicus* Fischer-Piette &

Bedoucha, 1965; streptaxids; *Sitala* H. Adams, 1865; and other pulmonates) (Emberton, 1997); (d) there is evidence that lowlands are richer than highlands in endemic and rare species (Emberton, 1997); and the small land snails (e) are sensitive ecological indicators of mild forest degradation from selective cutting or nearby slash-and-burn, and (f) do not seem to compete with congeners via shell size (Pearce & Emberton, unpublished).

All of those conclusions were based on undocumented morphospecies. This paper is the first in a series of four papers that identify and describe the species. This paper treats the Mahermana-Ilapiry-Vasiha caenogastropods.

In the interests of conservation in Madagascar, it is important to provide as much Red-List data (IUCN, 1996) as possible. In this paper, we evaluate the conservation statuses of the 17 *Boucardicus* species described herein.

MATERIALS AND METHODS

Collecting methods have been detailed by Emberton et al. (1996). Sixteen stations were collected and numbered in the "Tol" series (for Tolagnaro = Fort Dauphin, the nearest city). These stations have been mapped by Emberton et al. (1996, 1999) and in Emberton (1997). To

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shorten the taxonomic descriptions, stations are described briefly below. Station numbers are in the series of the Molluscan Biodiversity Institute (MBI). All stations were restricted to primary forest that had no more than limited selective cutting. Ecological data are given by Emberton (1997:table 1). All stations are in Madagascar: Tulear Province. Mount Mahermana (Vohimena Chain) is north-east of the village of Esetra, Ilapiry (Vohimena Chain) is west of Mahialambo, and Vasiha (Anosy Chain) is west of Malio. Latitude and longitude are given in degrees, minutes, and seconds.

MBI 373 (= Tol-1). Summit of Mt. Mahermana, 340 m, 24°26'12"S, 47°13'13"E.

MBI 374 (= Tol-2). Slope of Mt. Mahermana, 300 m, 24°26'17"S, 47°13'10"E.

MBI 375 (= Tol-3). Slope of Mt. Mahermana, 200 m, 24°26'15"S, 47°13'04"E.

MBI 376 (= Tol-4). Valley on Mt. Mahermana, 100 m, 24°26'22"S, 47°12'41"E.

MBI 377 (= Tol-5). Summit of Mt. Ilapiry, 540 m, 24°51'40"S, 47°00'20"E.

MBI 378 (= Tol-6). Ridge on Mt. Ilapiry, 500 m, 24°51'33"S, 47°00'27"E.

MBI 379 (= Tol-7). Ridge, valley, and slope on Mt. Ilapiry, 400 m, 24°51'27"S, 47°00'38"E.

MBI 380 (= Tol-8). Slope of Mt. Ilapiry, 300 m, 24°51'36"S, 47°00'40"E.

MBI 381 (= Tol-9). Slope of Mt. Ilapiry, 200 m, 24°51'39"S, 47°00'46"E.

MBI 382 (= Tol-10). Lower summit of Mt. Vasiha, 860 m, 24°55'18"S, 46°44'19"E.

MBI 383 (= Tol-11). Slope of Mt. Vasiha, 700 m, 24°55'23"S, 46°44'27"E.

MBI 384 (= Tol-12). Slope of Mt. Vasiha, 500 m, 24°55'19"S, 46°44'45"E.

MBI 385 (= Tol-13). Valley on Mt. Vasiha, 400 m, 24°55'25"S, 46°44'45"E.

MBI 386 (= Tol-14). Slope of Mt. Vasiha, 300 m, 24°55'37"S, 46°44'49"E.

MBI 387 (= Tol-15). Slope of Mt. Vasiha, 200 m, 24°56'13"S, 46°45'13"E.

MBI 388 (= Tol-16). Slope of Mt. Vasiha, 100 m, 24°56'20"S, 46°46'07"E.

MBI 389 (= Tol-3-4). Incidental collecting between Tol-3 and Tol-4.

MBI 390 (= Tol-1-2). Incidental collecting between Tol-1 and Tol-2.

MBI 391 (= Tol-sub-5). Incidental collecting below summit of Mt. Ilapiry, Tol-5.

MBI 392 (= Tol-7-9). Incidental collecting between Tol-7 and Tol-9.

Species identifications and comparisons were made using Fischer-Piette et al. (1993) and Emberton (1994, 1998). All caenogastropod species were identified, but, as Madagascar's large caenogastropod species are either fairly well known (Fischer-Piette et al., 1993) or—in the

case of large *Tropidophora*—in taxonomic chaos (Emberton, 1995), descriptions were prepared only for the small species.

For each small species, the holotype or a representative shell was photographed in apertural, basal, and side views at either $\times 10$, $\times 16$, $\times 25$, or $\times 40$ magnification, and in apical view at $\times 40$ magnification. Additional specimens were photographed as needed to illustrate shell variation or ontogeny.

Fifty-eight shell characters (Table 1, Figure 1) were measured, or measured and calculated, or scored from the photographs or from the shells themselves.

At least one adult male or female anatomy was available for 12 (71%) of the *Boucardicus* species. From each of these species, one to three reproductive systems were removed and illustrated by photographs and/or camera-lucida drawings as they were turned and progressively dissected to expose characters in the penis and FPSC (fertilization pouch-seminal receptacle complex). Only the penis and FPSC were examined because of time constraints and because these two organs seemed most likely to contain informative characters, based on previous experience. Seventeen reproductive-anatomical characters (Table 1, Figures 26–31) were taken from the drawings or from the dissections themselves.

Character matrices were prepared (available from K.C.E. on request) and were used to code character-state data into the DELTA system (Partridge et al., 1993; Dallwitz et al., 1993), which was then used to generate natural-language species descriptions. Computer-assisted taxonomic descriptions and keys have been developed over the years by a number of approaches (e.g., Pankhurst, 1975; Watson et al., 1986), arguably culminating in the DELTA system (Partridge et al., 1993; Dallwitz et al., 1993). DELTA is "a flexible data-coding format for taxonomic descriptions, and an associated set of programs for producing and typesetting natural-language descriptions and keys, for interactive identification and information retrieval, and for conversion of data to formats required for phylogenetic and phenetic analysis" (Partridge et al., 1993).

For each *Boucardicus* species, conservation status was evaluated using the latest categories and criteria of the International Union for the Conservation of Nature (IUCN, 1996). Ranges were estimated from distribution data in Emberton (in press). Rainforest extent and decline were assessed using Green & Sussman (1990), Sussman et al. (1994), and the most recently available topographic maps.

INFERENCE OF HOMOLOGIES

Interpretations of shell homologies were straightforward. Penis width was ruled out as a character, because during mating it can be drastically swollen (Figure 38 versus Figure 37). In the FPSC (fertilization pouch-seminal re-

Table 1

Shell and reproductive characters used in descriptions.

SHELL

1. Diameter (0.1 mm)
2. Height (0.1 mm)
3. Height/Diameter (0.1)
4. Spire angle (degrees)
5. Whorl periphery shape (round, angular, keeled)
6. Whorl shoulder shape (round, flat)
7. Aperture width parallel to parietal callus (% diameter)
8. Aperture height (perpendicular to parietal callus)/width (0.01)
9. Columellar plica (yes, no)
10. Aperture-plane inclination upward from rotational axis (5 degrees)
11. Apertural anal notch depth (% apertural width)
12. Baso-columellar denticle size (% apertural width)
13. Baso-columellar denticle depth (0.05 whorl)
14. Basal denticle size (% apertural width)
15. Basal denticle depth (0.05 whorl)
16. Upper palatal denticle size (% apertural width)
17. Upper palatal denticle depth (0.05 whorl)
18. Peristome angle of greatest dimension outward from rotational axis (5 degrees)
19. Peristome greater dimension/aperture width in same direction (0.01)
20. Peristome greatest dimension/lesser, perpendicular dimension (0.01)
21. Peristome baso-palatal indentation (% basal peristome width)
22. Peristome upper curl forward extension (% upper peristome width)
23. Inner, second peristome (none, projecting up to 0.01 whorl, projecting up to 0.05 whorl)
24. Umbilicus size pre-constriction (% diameter)
25. Umbilicus size total (% diameter)
26. Whorl number (0.1)
27. Embryonic whorl number (0.1)
28. Embryonic whorl sculpture
29. First whorl diameter (0.01 mm)
30. First three whorls diameter (0.01 mm)
31. Penult-whorl complete spiral grooves depth (0.01 mm)
32. Penult-whorl complete spiral grooves number between sutures
33. Penult-whorl spiral ridges height (0.01 mm)
34. Penult-whorl spiral ridges number between sutures
35. Penult-whorl spiral grooves or ridges waviness (none, slight, moderate)
36. Penult-whorl transverse ribs height (0.01 mm)
37. Penult-whorl transverse ribs number in last 0.1 whorl
38. Penult-whorl herringbone sculpture (Figures 4, 10) number in last 0.1 whorl
39. Penult-whorl honeycomb sculpture (Figure 19) number per 0.1 whorl
40. Penult-whorl short spiral grooves number between sutures
41. Penult-whorl short spiral grooves length (0.01 mm)
42. Penult-whorl spiral lines of punctae number between sutures
43. Penult-whorl spiral lines of punctae number per 0.1 whorl
44. Pre-apertural constriction distance from aperture (0.1 whorl)
45. Pre-apertural constriction (% whorl diameter constriction)
46. Pre-constriction diminution of sculpture (%)

Table 1

Continued.

47. Post-constriction immediate percent diameter swelling (%)
48. Post-constriction secondary constriction (yes, no)
49. Post-secondary constriction swelling (% diameter of first constriction)
50. Pre-apertural transverse ribs height (0.01 mm)
51. Pre-apertural transverse ribs procumbancy angle
52. Pre-apertural transverse ribs number per 0.1 whorl
53. Color general
54. Color apex
55. Spiral color band number
56. Spiral color band color
57. Preapertural constriction color
58. Peristome color (excluding periostracum)

PENIS

59. Length (0.1 mm)
60. Length/ shell diameter (0.1)
61. Terminal papilla-ejaculatory pore position (dorsal, central, ventral)
62. Dorsal papilla-ejaculatory pore position (terminal, subterminal)
63. Papilla protrusion (none, slight, strong)
64. Papilla direction (anterior, posterior)
65. Swelling at tip of penis: swelling width/pre-swelling width (0.1)
66. Gland (present, absent)
67. Gland length/pre-swelling penial width (0.1)
68. Gland proximal-distal position: distance from base of penis to midpoint of gland/penial length (0.1)
69. Gland dorsal-ventral attachment position (dorsal, ventral)
70. Gland free-lobe direction (left, right)

FPSC (FERTILIZATION POUCH-SEMINAL RECEPTACLE COMPLEX)

71. Base (present, absent)
72. Base shape
73. Base ducted gland (present, absent)
74. Body-interior muscular funnel (present, absent)
75. Body-and-tube shape

ceptacle) great morphological diversity (Figures 27–31, 55–68) called for some judgment. Internal structures of two disparate morphologies (Figures 53, 54) led to the hypothesis of three distinct regions of the *Boucardicus* FPSC (Figures 27–31). The *base* appears to be lined with glandular tissue, and it may or may not have additional glandular lobes, or an appendage, or a ducted or ductless gland; the shape of the base varies from globular to thin and elongate; *Cyathopoma* seems to lack a base. The FPSC *body* seems to be a muscular tube that may or may not contain a muscular, funnel-shaped organ (Figure 54). Apically (i.e., proximally), the body grades into a thinner-walled *tube*; the gradation can be abrupt or gradual.

SYSTEMATICS

Higher classification follows Ponder & Lindberg (1997) and Vaught (1989). Type materials are placed in the Unit-

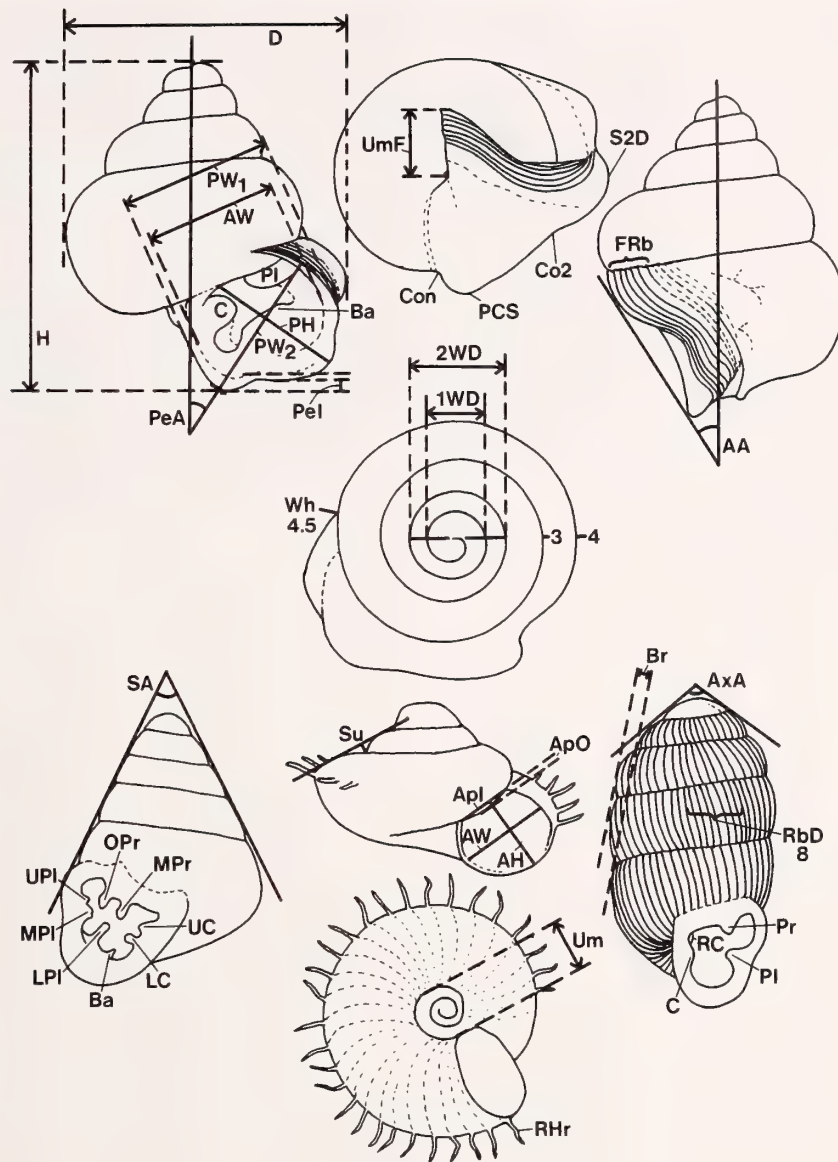


Figure 1

Some of the shell features measured, scored, and used in calculating characters (Table 1), shown on *Boucardicus* (above) and some pulmonates (below). 1WD, first whorl diameter; 2WD, first two whorls diameter; AA, angle at which apertural plane is inclined from rotational axis; AH, aperture height (inside dimension measured to and perpendicular to a line between columellar and upper peristome insertions); ApI, distance between the columellar and upper peristome insertions; ApO, amount of aperture occupied by previous whorl; AW, aperture width (inside dimension measured parallel to a line between the columellar and upper peristome insertions); AxA, apex angle; Ba, basal denticle; Br, barreling (outward departure from a straight line of a tangent to the whorls between n-0.5 and about the second whorl); C, columellar denticle; Co2, second body whorl constriction; Con, body whorl constriction; D, shell diameter; FRb, final ribs near body whorl aperture; H, shell height; LC, lower columellar denticle; LPI, lower palatal denticle; MPI, middle palatal denticle; MPr, middle parietal denticle; OPr, outer parietal denticle; PCS, post-constrictional body whorl swelling; PeA, angle from greatest width of aperture plus peristome to rotational axis; PeI, peristome baso-palatal indentation (expressed as percent of basal peristome width, i.e., to the unlabelled line above it in the figure); PH, aperture plus peristome greatest height as measured perpendicular to greatest width line; PI, palatal denticle; Pr, parietal denticle; PW1, aperture plus peristome width (measured parallel to aperture width); PW2, aperture plus peristome greatest width (measured on *Boucardicus*, parallel to or within 40 degrees of parietal-callus line); RbD, transverse rib density (number in estimated tenth of whorl); RC, recessed columellar denticle; RHr, rib hairs; S2D, swelling after second body whorl constriction; SA, spire angle; Su, suture depth one half whorl from aperture; UC, upper columellar denticle; Um, umbilicus size before any change in body whorl growth direction; UmF, final umbilicus total size; UPI, upper palatal denticle; Wh, whorl number.

ed States National Museum, Washington, D.C. (USNM); temporarily in the Molluscan Biodiversity Institute (MBI), all of whose collections will revert in the near future to USNM; and in the Australian Museum, Sydney (AMS); the Muséum National d'Histoire Naturelle, Paris (MNHN); and the Academy of Natural Sciences of Philadelphia (ANSP). MBI catalog numbers consist of station number (see Methods section), reference number of the species, D (dry) or A (alcohol-preserved), and when appropriate H (holotype) or P (paratype) or R (representative).

Class GASTROPODA

Clade CAENOGASTROPODA

Superfamily CYCLOPHOROIDEA

Family CYCLOPHORIDAE

Genus *Boucardicus* Fischer-Piette & Bedoucha, 1965

New Synonym: *Madecataulus* Fischer-Piette & Bedoucha, 1965 (type species *Madecataulus goudoti* Fischer-Piette & Bedoucha, 1965). The operculum and preapertural constriction and swelling of *Madecataulus* are virtually identical to those of *Boucardicus* (Emberton, 1994). The high spire seems insufficient to define a distinct genus.

Boucardicus esetrae Emberton & Pearce, sp. nov.

(Figures 2, 29, 33, 55)

Boucardicus n. sp. 19, Emberton, 1996:735.

Boucardicus sp. 1, Emberton et al., 1996:210. Emberton, 1997:1146, 1149. Emberton et al., 1999:table 2.

Holotype: USNM 860776 (ex MBI 382.01DH, adult shell).

Paratypes: MBI 374.05DP (1 adult, 1 juvenile), MBI 377.05DP (1 ad, 1 juv), MBI 378.07DP (1 juv), MBI 378.07AP (1 juv), MBI 380.05DP (1 ad), MBI 380.05AP (1 juv), MBI 382.01DP (41 ad, 66 juv; AMS C.203419 [1 ad], MNHN [1 ad], ANSP 400821 [1 ad]), MBI 382.01AP (5 ad [2 dissected], 12 juv), MBI 383.05DP (13 ad, 18 juv), MBI 383.05AP (2 juv), MBI 384.08DP (2 ad, 2 juv), MBI 385.03DP (15 ad, 15 juv), MBI 385.03AP (2 ad [1 dissected]).

Type locality: Madagascar: Tulear Province: northwest of Fort Dauphin: west of village of Malio: local summit of Mount Vasiha, south of main summit, 860 m elevation: latitude 24°55'18"S, longitude 46°44'19"E: primary rain-forest.

Description of holotype shell:

Size and Shape. Diameter 3.9 mm; height 4.6 mm. Height-diameter ratio 1.2. Spire angle 70 degrees. Whorl periphery round. Whorl shoulder round. Umbilicus before

body whorl constriction 0% of shell diameter. Final umbilicus 15% of shell diameter. Whorls 5.4.

Aperture. Aperture width parallel to parietal callus 41% of shell diameter. Aperture height-width ratio (height measured perpendicular to parietal callus) 0.94. Columellar plica absent. Apertural plane parallel to rotational axis. No apertural anal notch. No baso-columellar denticle. No basal denticle. No upper palatal denticle. Ratio of aperture plus peristome greatest width (measured parallel to or within 40 degrees of parietal-callus line) to aperture width 1.64. Aperture plus peristome greatest dimension angled outward from rotational axis 30 degrees. Ratio of aperture plus peristome greatest width to aperture plus peristome greatest height as measured perpendicular to width line 1.26. No peristome baso-palatal indentation. No peristome upper curl forward extension. Inner, second peristome present, projecting less than 0.01 whorl.

Apex. Embryonic whorls 2.1. Embryonic sculpture granular. First whorl diameter 0.55 mm. First three whorls diameter 1.56 mm.

Sculpture on Last Tenth of Penultimate Whorl. Transverse ribs 24; rib height 0.3% of shell diameter. No complete spiral grooves between sutures. No short spiral grooves between sutures. No spiral ridges between sutures. No spiral lines of punctae between sutures. No heringbone sculpture; no honeycomb sculpture.

Pre-Apertural Morphology. Body whorl constricted 0.2 whorl before aperture; constricting by 4% of whorl diameter. Body whorl sculpture not diminishing before constriction. Post-constriction body whorl swollen by 2% of constriction diameter. No secondary body whorl constriction. Transverse ribs on post-constrictional swelling numbering 8 in 0.1 whorl; rib height 0.3% of shell diameter; ribs not slanted.

Color. Basic color brown-orange. Apex brown-orange. One spiral color band; color white. Pre-apertural constriction red-brown. Peristome (excluding periostracum) white.

Shell variation: Younger, fresher shells have—in addition to the described rib sculpture—regularly, widely spaced, high-standing periostracal transverse ribs. Some adults have a slightly broader outer peristome than the holotype. During shell growth, the outer peristome forms first, so neoadults lack the inner peristome. Color varies from brown to yellow-brown. Among the 44 adults from station MBI-382, shell height ranges from 4.7 to 5.9 mm.

Shell comparisons: Half the size of *Boucardicus albocinctus* (Smith, 1893) and *B. antsahanori* Emberton, 1994. Larger than *B. mageti* Fischer-Piette, Blanc, Blanc & Salvat, 1993, and without its spiral striation. Younger, fresher shells are unique within the genus for their regularly, widely spaced, high-standing periostracal transverse ribs.



Explanation of Figures 2–4

Shells of Mahermana-Ilapiry-Vasiha *Boucardicus*. Figure 2. *Boucardicus esetrae* Emberton & Pearce, sp. nov., holotype. Figure 3. *Boucardicus antiquus* Emberton & Pearce, sp. nov., holotype. Figure 4. *Boucardicus delicatus* Emberton & Pearce, sp. nov., holotype. All scale bars 1 mm.

Description of genitalia (MBI 382.01AP: 1 male, 1 female; MBI 385.03AP: 1 female): Penis length 2.8 mm, 0.7 shell diameter. Penial papilla-ejaculatory-pore position dorsal. Penial dorsal papilla terminal, weak to no protrusion beyond tip of penis, anteriorly directed. Penis terminal swelling conspicuous, terminal-bulb width 1.3 pre-bulb width. Penial gland present. Penial-gland length 1.3 penis pre-terminal-bulb width. Penial-gland position proximal, its center 0.4 along the penis length from its base. Penial-gland attachment position dorsal. Penial-gland free lobe direction left. Base of FPSC (fertilization pouch-seminal receptacle complex): broad-based, simple. Ducted gland on base of FPSC absent. Muscular funnel within body of FPSC present. Body-and-tube shape of FPSC: upper body straight, apex-plus-tube a rounded, up-pointed, backward "S."

Distribution: On all three mountains, from 300 to 860 m elevation. Also apparently on Pic St. Louis (25°00'30"S, 46°57'45"E) at 500–530 m, and on Mounts Vohibololo (340–420 m) and Teloboko (640 m) near Mount Mahermana (MBI 1419, 1420, 1438–1440, 1451), all in the Vohimena Chain; in the Anosy Chain, not found north of Mount Vasiha on either Andohahela or Col Beampingaratra; no other records exist (Emberton, in press). Thus, restricted to the Vohimena and the southern Anosy chains, with a range extent of < 1,000 km², with severely fragmented populations, and within forest habitat that is continuing to decline in extent and/or quality. Meets IUCN (1996) criteria for Endangered status.

Etymology: For the village of Esetra, near the type locality.

Boucardicus antiquus Emberton & Pearce, sp. nov.

(Figures 3, 34, 56)

Boucardicus n. sp. 17, Emberton, 1996:735.

Boucardicus sp. 2, Emberton et al., 1996:210. Emberton, 1997:1146, 1149. Emberton et al., 1999:table 2.

Holotype: USNM 860777 (ex MBI 387.01DH, adult shell).

Paratypes: MBI 373.13DP (1 ad, 4 juv), MBI 373.13AP (1 ad), MBI 375.05DP (1 ad), MBI 376.05DP (1 juv), MBI 376.05AP (2 ad), MBI 377.06DP (1 ad, 1 juv), MBI 378.08DP (1 ad, 1 juv), MBI 379.08DP (6 ad, 4 juv), MBI 379.08AP (2 ad, 2 juv), MBI 380.06DP (1 ad), MBI 385.04DP (1 juv), MBI 386.06DH (4 ad, 3 juv), MBI 386.06AP (2 ad, 2 juv), MBI 387.01DP (10 ad, 16 juv; AMS C.203420 [1 ad]; MNHN [1 ad]; ANSP 400822 [1 ad]), MBI 387.01AP (4 ad [2 dissected], 2 juv), MBI 390.01DP (1 ad, 1 juv).

Type locality: Madagascar: Tulear Province: northwest of Fort Dauphin: west of village of Malio: eastsoutheast-facing slope of Mount Vasiha, 200 m elevation: latitude 24°56'13"S, longitude 46°45'13"E: primary rainforest.

Description of holotype shell:

Size and Shape. Diameter 3.2 mm; height 5.5 mm. Height-diameter ratio 1.7. Spire angle 65 degrees. Whorl periphery round. Whorl shoulder round. Umbilicus before body whorl constriction 0% of shell diameter. Final umbilicus 5% of shell diameter. Whorls 6.5.

Aperture. Aperture width parallel to parietal callus 39% of shell diameter. Aperture height-width ratio (height measured perpendicular to parietal callus) 1.00. Columellar plica present. Apertural plane inclined downward; 5 degrees from rotational axis. Apertural anal notch 26% of apertural width. No baso-columellar denticle. No basal denticle. No upper palatal denticle. Ratio of aperture plus peristome greatest width (measured parallel to or within 40 degrees of parietal-callus line) to aperture width 1.74. Aperture plus peristome greatest dimension angled outward from rotational axis 35 degrees. Ratio of aperture plus peristome greatest width to aperture plus peristome greatest height as measured perpendicular to width line 1.28. No peristome baso-palatal indentation. No peristome upper curl forward extension. Inner, second peristome present, projecting more than 0.01 whorl.

Apex. Embryonic whorls 2.2. Embryonic sculpture smooth then transverse ribs. First whorl diameter 0.54 mm. First three whorls diameter 1.06 mm.

Sculpture on Last Tenth of Penultimate Whorl. Transverse ribs 11; rib height 0.9% of shell diameter. No complete spiral grooves between sutures. No short spiral grooves between sutures. No spiral ridges between sutures. No spiral lines of punctae between sutures. No herringbone sculpture; no honeycomb sculpture.

Pre-Apertural Morphology. Body whorl constricted 0.6 whorl before aperture; constricting by less than 0.5% of whorl diameter. Body whorl sculpture diminishes 90% before constriction. Post-constriction body whorl swollen by 26% of constriction diameter. No secondary body whorl constriction. Transverse ribs on post-constrictional swelling numbering 11 in 0.1 whorl; rib height 0.9% of shell diameter; ribs not slanted.

Color. Basic color white. Apex white. No spiral color bands. Pre-apertural constriction white. Peristome (excluding periostracum) white.

Shell variation: As in *Boucardicus esetrae* sp. nov., the outer peristome forms first, so some neoadults lack the inner peristome. No other conspicuous variation in shape or size.

Shell comparisons: Shorter than *Boucardicus villae* (Fischer-Piette, Blanc, Blanc & Salvat, 1993) and with a narrower apertural anal notch and a much greater preapertural swelling of the body-whorl. With a smaller aperture than *B. fauri* (Fischer-Piette, Blanc, Blanc & Salvat, 1993), greater preapertural swelling, lesser umbilical major spiral ridge, and without any forward curl of the upper peristome.

Description of reproductive characters (MBI 387.01AP: 1 male, 1 female): Penis length 2.2 mm, 0.7 shell diameter. Penial papilla-ejaculatory-pore position dorsal. Penial dorsal papilla subterminal. Penis terminal swelling conspicuous, terminal-bulb width 1.4 pre-bulb width. Penial gland present. Penial-gland length 0.6 penis pre-terminal-bulb width. Penial-gland position proximal, its center 0.4 along the penis length from its base. Penial-gland attachment position dorsal. Penial-gland free lobe direction undetectable. Base of FPSC (fertilization pouch-seminal receptacle complex) broad-based, simple. Ducted gland on base of FPSC absent. Muscular funnel within body of FPSC absent. Body-and-tube shape of FPSC: upper body straight, apex-plus-tube a rounded, up-pointed, backward "S."

Distribution: On all three mountains, 100–600 m elevation and below. Also apparently on Pic St. Louis (25°00'30"S, 46°57'45"E) at 380–530 m, and on Mounts Vohibololo (110–310 m), Teloboko (530–640 m), and Esetra (summit), near Mount Mahermana (MBI 1419, 1424, 1436, 1441–1443, 1451–1453, 1493), all in the Vohimena Chain; in the Anosy Chain, found on Andohahela (430–600 m: MBI 799, 1659) but not Col Beampingaratra; outside the Vohimena-Anosy region, *Boucardicus antiquus* sp. nov. ranges northward, having been found east of Midongy at 80 m (23°23'20"S, 47°20'02"E), east of Andringitra Reserve at 1400 m (22°04'S, 46°54'E), and at Kianjavato at 200–430 m (21°22'20"S, 47°52'05"E) (MBI 1375, 1402, 1380, 1387), but not north of Kianjavato (Emberton, in press). Thus, this species is apparently restricted to the southern third of Madagascar's eastern rainforest, with a range extent of well under 20,000 km², with severely fragmented populations, and within forest habitat that is continuing to decline in extent and/or quality. Meets IUCN (1996) criteria for Vulnerable status.

Etymology: Named for the antique (Latin *antiquus*) appearance of the shell.

Boucardicus delicatus Emberton & Pearce, sp. nov.

(Figures 4, 35, 57)

Boucardicus sp. 3, Emberton et al., 1996:210. Emberton, 1997:1147. Emberton et al., 1999:table 2.

Holotype: USNM 860778 (ex MBI 385.01DH, adult shell).

Paratypes: MBI 379.09DP (1 ad), MBI 379.09AP (2 ad, 1 juv), MBI 381.07DP (1 ad, 1 juv), MBI 382.08DP (1 ad), MBI 384.09DP (1 ad), MBI 385.01DP (1 ad, 2 juv; AMS C.203421 [1 ad]; MNHN [1 ad]), MBI 385.01AP (3 ad [2 dissected], 2 juv), MBI 386.07DP (2 ad).

Type locality: Madagascar: Tulear Province: northwest of Fort Dauphin: west of village of Malio: eastsoutheast-facing valley on Mount Vasiha, 400 m elevation: latitude 24°55'25"S, longitude 46°44'45"E: primary rainforest.

Description of holotype shell:

Size and Shape. Diameter 1.1 mm; height 1.8 mm. Height-diameter ratio 1.7. Spire angle 65 degrees. Whorl periphery round. Whorl shoulder round. Umbilicus before body whorl constriction 0% of shell diameter. Final umbilicus 0% of shell diameter. Whorls 4.6.

Aperture. Aperture width parallel to parietal callus 37% of shell diameter. Aperture height-width ratio (height measured perpendicular to parietal callus) 1.09. Columellar plica absent. Apertural plane inclined downward; 5 degrees from rotational axis. No apertural anal notch. Baso-columellar denticle present; size 25% of apertural width; depth 0.00 whorl. No basal denticle. No upper palatal denticle. Ratio of aperture plus peristome greatest width (measured parallel to or within 40 degrees of parietal-callus line) to aperture width 1.81. Aperture plus peristome greatest dimension angled outward from rotational axis 50 degrees. Ratio of aperture plus peristome greatest width to aperture plus peristome greatest height as measured perpendicular to width line 1.14. Peristome baso-palatal indentation 50% of basal peristome width. No peristome upper curl forward extension. Inner, second peristome absent.

Apex. Embryonic whorls 2.0. Embryonic sculpture smooth. First whorl diameter 0.30 mm. First three whorls diameter 0.76 mm.

Sculpture on Last Tenth of Penultimate Whorl. No transverse ribs. No complete spiral grooves between sutures. No short spiral grooves between sutures. No spiral ridges between sutures. No spiral lines of punctae between sutures. Fourteen herringbones; no honeycomb sculpture.

Pre-Apertural Morphology. Body whorl constricted 0.3 whorl before aperture; constricting by 4% of whorl diameter. Body whorl sculpture not diminishing before constriction. Post-constriction body whorl swollen by 21% of constriction diameter. No secondary body whorl constriction. Transverse ribs on post-constrictional swelling numbering 10 in 0.1 whorl; rib height less than 0.05% of shell diameter; ribs not slanted.

Color. Basic color white-brown. Apex brown-white. No spiral color bands. Pre-apertural constriction white-brown. Peristome (excluding periostracum) white.

Shell variation: No conspicuous variation in size or shape.

Shell comparisons: Unique in its combination of minute size, high-spined shape, and herringbone sculpture. Most similar to *Boucardicus randalanai* sp. nov., from which it differs in its smaller, more ovate aperture.

Description of reproductive characters (MBI 387.01AP: 1 male, 1 female): Penis length 0.9 mm, 0.8 shell diameter. Penial papilla-ejaculatory-pore position central. Penis terminal swelling slight, terminal-bulb width 1.1 pre-bulb width. Penial gland absent. Base of

FPSC (fertilization pouch-seminal receptacle complex) undetectable. Ducted gland on base of FPSC absent. Body-and-tube shape of FPSC: upper body straight, apex-plus-tube a rounded, up-pointed, backward "S."

Local distribution: On Mounts Ilapiry and Vasiha, 200–400 m elevation. Not found in the northern Vohimena chain; also found on Andohahela, 430–1600 m (MBI 771, 772, 780, 781, 789, 791, 799), but not at Col Beampingaratra (Emberton, in press). Thus, apparently restricted to the southern Anosy and Vohimena chains, with a range extent < 1,000 km², with severely fragmented populations, and within forest habitat that is continuing to decline in extent and/or quality. Meets IUCN (1996) criteria for Endangered status.

Etymology: The tiny shell is very thin and fragile (Latin *delicatus*).

Boucardicus curvifolius Emberton & Pearce,
sp. nov.

(Figures 5, 36, 58)

Boucardicus n. sp. 21, Emberton, 1996:735.

Boucardicus sp. 4, Emberton et al., 1996:210. Emberton, 1997:1146, 1149. Emberton et al., 1999:table 2.

Holotype: USNM 860779 (ex MBI 381.01DH, adult shell).

Paratypes: MBI 373.22AP (2 ad), MBI 377.21AP (1 ad), MBI 379.32AP (3 ad), MBI 380.07DP (1 ad), MBI 380.07AP (7 ad [1 dissected], 1 juv), MBI 381.01DP (3 ad; AMS C.203422 [1 ad]; MNHN [1 ad]; ANSP 400823 [1 ad]), MBI 381.01AP (2 ad [2 dissected], 3 juv).

Type locality: Madagascar: Tulear Province: north of Fort Dauphin: west of village of Mahialambo: east-south-east-facing slope of Mount Ilapiry, 200 m elevation: latitude 24°51'39"S, longitude 47°00'46"E: primary rainforest.

Description of holotype shell:

Size and Shape. Diameter 3.5 mm; height 3.2 mm. Height-diameter ratio 0.9. Spire angle 70 degrees. Whorl periphery round. Whorl shoulder round. Umbilicus before body whorl constriction 0% of shell diameter. Final umbilicus 16% of shell diameter. Whorls 4.2.

Aperture. Aperture width parallel to parietal callus 31% of shell diameter. Aperture height-width ratio (height measured perpendicular to parietal callus) 0.88. Columellar plica absent. Apertural plane inclined upward; 10 degrees from rotational axis. No apertural anal notch. No baso-columellar denticle. No basal denticle. No upper palatal denticle. Ratio of aperture plus peristome greatest width (measured parallel to or within 40 degrees of parietal-callus line) to aperture width 2.18. Aperture plus peristome greatest dimension angled outward from rotational axis 15 degrees. Ratio of aperture plus peristome

greatest width to aperture plus peristome greatest height as measured perpendicular to width line 1.51. Peristome baso-palatal indentation 42% of basal peristome width. Peristome upper curl extends forward 82% of upper peristome width. Inner, second peristome present, projecting less than 0.01 whorl.

Apex. Embryonic whorls 2.0. Embryonic sculpture smooth with faint traces of growth lines. First whorl diameter 0.74 mm. First three whorls diameter 1.98 mm.

Sculpture on Last Tenth of Penultimate Whorl. No transverse ribs. No complete spiral grooves between sutures. No short spiral grooves between sutures. No spiral ridges between sutures. No spiral lines of punctae between sutures. No herringbone sculpture; no honeycomb sculpture.

Pre-Apertural Morphology. Body whorl constricted 0.4 whorl before aperture; constricting by 11% of whorl diameter. Lack of body whorl sculpture continues into constriction. Post-constriction body whorl swollen by 11% of constriction diameter. Secondary body whorl constriction present; swelling after secondary constriction enlarged by 34% of diameter of first constriction. Transverse ribs on post-constrictional swelling numbering 14 in 0.1 whorl; rib height 1.4% of shell diameter; ribs slanting backward; 60 degrees.

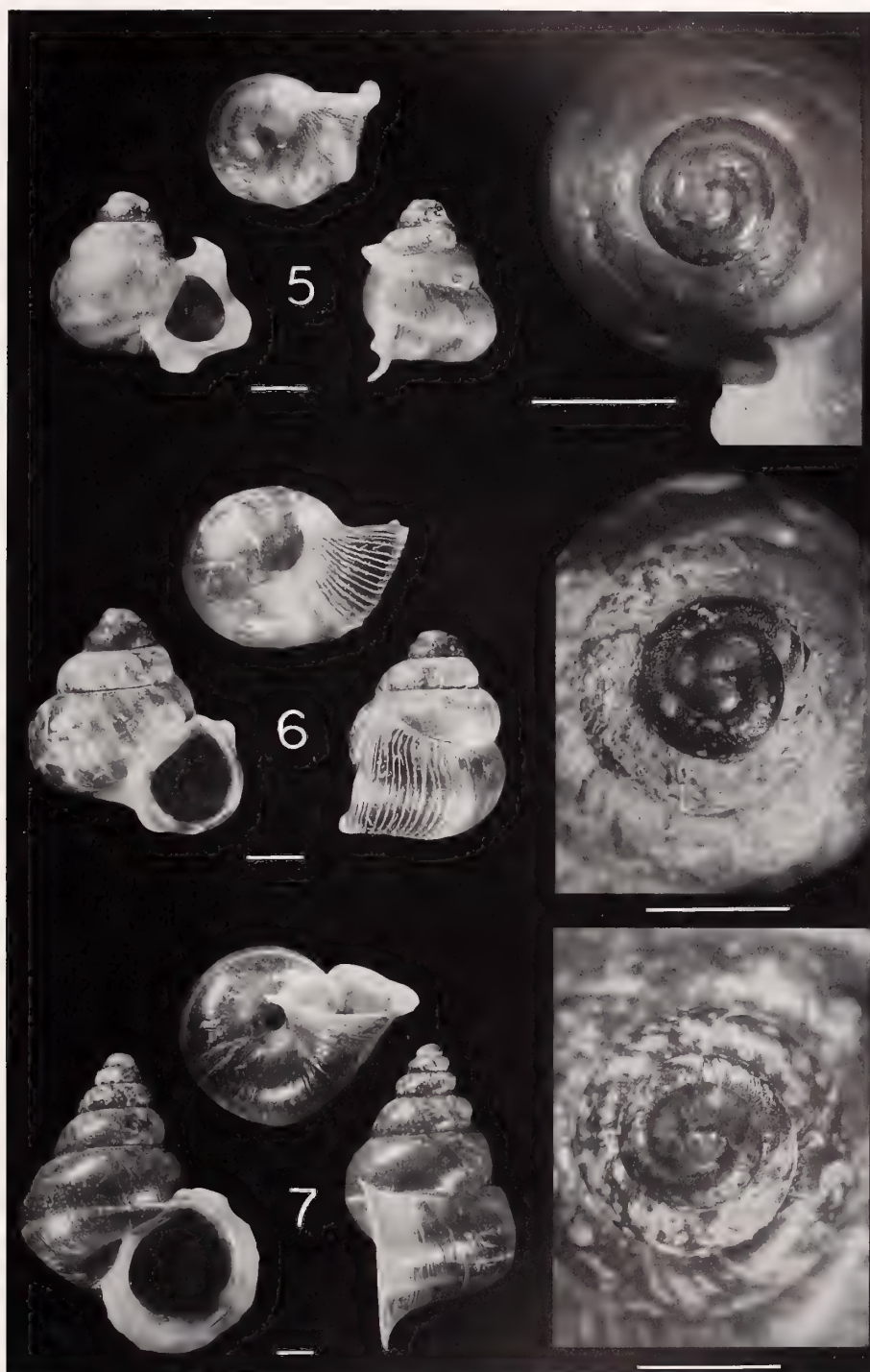
Color. Basic color brown. Apex red-brown. Two spiral color bands; color yellow-white. Pre-apertural constriction yellow-white. Peristome (excluding periostracum) yellow-white.

Shell variation: No conspicuous variation in size or shape.

Shell comparisons: Unique in its flamboyantly tri-lobed apertural peristome.

Description of reproductive characters (MBI 380.07AP: 1 male; MBI 381.01AP: 1 male, 1 female): Penis length 2.5 mm, 0.7 shell diameter. Penial papilla-ejaculatory-pore position dorsal. Penial dorsal papilla terminal, weak to no protrusion beyond tip of penis, anteriorly directed. Penis terminal swelling slight, terminal-bulb width 1.2 pre-bulb width. Penial gland present. Penial-gland length 2.0 penis pre-terminal-bulb width. Penial-gland position distal, its center 0.8 along the penis length from its base. Penial-gland attachment position ventral. Penial-gland free lobe direction left. Base of FPSC (fertilization pouch-seminal receptacle complex) broad-based, simple. Ducted gland on base of FPSC absent. Muscular funnel within body of FPSC present. Body-and-tube shape of FPSC: upper mid-body folded left, apex-plus-tube a squashed, backward "S."

Distribution: Known only from the Vohimena chain (Mt. Mahermana and Mt. Ilapiry), from 200 to 540 m elevation. One other locality (Emberton, in press) is also in the Vohimena chain: Pic St. Jacques (24°58'00"S, 46°57'25"E), 520 m (MBI 1431). Thus, restricted to the



Explanation of Figures 5–7

Shells of Mahermana-Ilapiry-Vasiha *Boucardicus*. Figure 5. *Boucardicus curvifolius* Emberton & Pearce, sp. nov., holotype. Figure 6. *Boucardicus victorhernandezi* Emberton, 1998 b, holotype. Figure 7. *Boucardicus albocinctus* (Smith, 1893), representative from Mount Mahermana. All scale bars 1 mm.

Vohimena chain, with a range extent of < 500 km², with severely fragmented populations, and within forest habitat that is continuing to decline in extent and/or quality. Meets IUCN (1996) criteria for Endangered status.

Etymology: From the peristome resembling a curled (Latin *curvi-*) leaf (*L. folius*).

Boucardicus victorhernandezii Emberton, 1998

(Figures 6, 59)

Boucardicus sp. 5, Emberton et al., 1996:210. Emberton, 1997:1147. Emberton et al., 1999:table 2.

Description of holotype shell (from Emberton, 1998):

"Size and Shape. Diameter 3.7 mm; height 3.8 mm. Height-diameter ratio 1.0. Spire angle 80 degrees. Whorl periphery round. Whorl shoulder round. Umbilicus before body whorl constriction 0% of shell diameter. Final umbilicus 29% of shell diameter. Whorls 4.5."

"Aperture. Aperture width parallel to parietal callus 38% of shell diameter. Aperture height-width ratio (height measured perpendicular to parietal callus) 0.87. Columellar plica absent. Apertural plane inclined upward; 5 degrees from rotational axis. No apertural anal notch. No baso-columellar denticle. No basal denticle. No upper palatal denticle. Ratio of aperture plus peristome greatest width (measured parallel to or within 40 degrees of parietal-callus line) to aperture width 1.54. Aperture plus peristome greatest dimension angled outward from rotational axis 35 degrees. Ratio of aperture plus peristome greatest width to aperture plus peristome greatest height as measured perpendicular to width line 1.32. Peristome baso-palatal indentation 23% of basal peristome width. Peristome upper curl extends forward 17% of upper peristome width. Inner, second peristome present, projecting less than 0.01 whorl."

"Apex. Embryonic whorls 2.0. Embryonic sculpture granular with faint traces of growth lines. First whorl diameter 0.75 mm. First three whorls diameter 2.10 mm."

"Sculpture on Last Tenth of Penultimate Whorl. Transverse ribs 22; rib height less than 0.05% of shell diameter. No complete spiral grooves between sutures. No short spiral grooves between sutures. No spiral ridges between sutures. No spiral lines of punctae between sutures. No herringbone sculpture; no honeycomb sculpture."

"Pre-Apertural Morphology. Body whorl constricted 0.3 whorl before aperture; constricting by 11% of whorl diameter. Body whorl sculpture not diminishing before constriction. Post-constriction body whorl swollen by 10% of constriction diameter. No secondary body whorl constriction. Transverse ribs on post-constrictional swelling numbering 10 in 0.1 whorl; rib height 1.1% of shell diameter; ribs slanting forward; 80 degrees."

"Color. Basic color brown-red. Apex dark brown-red. One spiral color band; color white. Pre-apertural constrict-

tion white. Peristome (excluding periostracum) white and red-brown."

Description of reproductive characters (MBI 373.23AP: 1 female): Penial morphology unknown. Base of FPSC (fertilization pouch-seminal receptacle complex) broad-based, simple. Ducted gland on base of FPSC absent. Muscular funnel within body of FPSC present. Body-and-tube shape of FPSC: upper mid-body folded left, apex-plus-tube a squashed, backward "S."

Distribution: Restricted to the Vohimena Mountain Chain; known from only four of eight sampled peaks within the chain; proposed for Endangered status (Emberton, 1998).

Boucardicus albocinctus (E. A. Smith, 1893)

(Figures 7, 28, 32, 37, 38, 49–51, 53, 61)

Boucardicus albocinctus (Smith, 1893), Emberton, 1996: 735.

Boucardicus sp. 6, Emberton et al., 1996:210. Emberton, 1997:1146, 1149. Emberton et al., 1999:table 2.

Representative: MBI 373.01DR (ad).

Other specimens: MBI 373.01D (0; AMS C.203424 [1 ad]), MBI 373.01A (3 Zad [2 dissected]), MBI 374.06D (1 ad, 2 juv), MBI 374.06A (1 ad), MBI 375.06D (1 juv), MBI 375.06A (1 juv), MBI 377.08D (2 ad), MBI 390.05A (2 ad).

Description of representative shell:

Size and Shape. Diameter 6.5 mm; height 8.2 mm. Height-diameter ratio 1.3. Spire angle 50 degrees. Whorl periphery round. Whorl shoulder round. Umbilicus before body whorl constriction 2% of shell diameter. Final umbilicus 9% of shell diameter. Whorls 5.9.

Aperture. Aperture width parallel to parietal callus 45% of shell diameter. Aperture height-width ratio (height measured perpendicular to parietal callus) 0.97. Columellar plica absent. Apertural plane parallel to rotational axis. No apertural anal notch. No baso-columellar denticle. No basal denticle. No upper palatal denticle. Ratio of aperture plus peristome greatest width (measured parallel to or within 40 degrees of parietal-callus line) to aperture width 1.68. Aperture plus peristome greatest dimension angled outward from rotational axis 40 degrees. Ratio of aperture plus peristome greatest width to aperture plus peristome greatest height as measured perpendicular to width line 1.24. No peristome baso-palatal indentation. Peristome upper curl extends forward 28% of upper peristome width. Inner, second peristome absent.

Apex. Embryonic whorls 2.0. Embryonic sculpture granular with faint traces of growth lines. First whorl diameter 0.78 mm. First three whorls diameter 1.88 mm.

Sculpture on Last Tenth of Penultimate Whorl. Transverse ribs 18; rib height 0.2% of shell diameter. Sixty complete spiral grooves between sutures; complete spiral

grooves slightly wavy. No short spiral grooves between sutures. No spiral ridges between sutures. No spiral lines of punctae between sutures. No herringbone sculpture; no honeycomb sculpture.

Pre-Apertural Morphology. Body whorl constricted 0.1 whorl before aperture; constricting by 4% of whorl diameter. Body whorl sculpture not diminishing before constriction. Post-constriction body whorl swollen by 0% of constriction diameter. No secondary body whorl constriction. Transverse ribs on post-constrictional swelling numbering 12 in 0.1 whorl; rib height 1.2% of shell diameter; ribs slanting forward; 90 degrees.

Color. Basic color brown-red. Apex dark brown-red. One spiral color band; color white. Pre-apertural constriction brown-red. Peristome (excluding periostracum) white and red-brown.

Local shell variation: The one adult from station MBI 374 has a more oval, less circular aperture than the representative.

Description of reproductive characters (MBI 373.01A: 1 male, 1 female [mating pair]): Penis length 5.6 mm, 0.9 shell diameter. Penial papilla-ejaculatory-pore position dorsal. Penial dorsal papilla terminal, weak to no protrusion beyond tip of penis, anteriorly directed. Penis terminal swelling conspicuous, terminal-bulb width 1.6 pre-bulb width. Penial gland present. Penial-gland length 1.2 penis pre-terminal-bulb width. Penial-gland position proximal, its center 0.3 along the penis length from its base. Penial-gland attachment position dorsal. Penial-gland free lobe direction right. Base of FPSC (fertilization pouch-seminal receptacle complex) narrow-based, with multiple apical lobes. Ducted gland on base of FPSC absent. Muscular funnel within body of FPSC absent. Body-and-tube shape of FPSC: upper mid-body folded left, apex-plus-tube a squashed, backward "S."

Distribution: On the two eastern, Vohimena-Chain mountains (Mts. Mahemana and Ilapiry) from 200 to 540 m elevation. Apparently a very wide-ranging species within Madagascar's eastern rainforest. Fischer-Piette et al. (1993) gave records from Périnet and Anosibe. Emberton (in press) reported it from many sites, including Andohahela and Beampingaratra in the Anosy chain, the northernmost of which is Betampona Reserve, northwest of Tamatave (17°55'05"S, 49°12'00"E), but no farther north. Thus, this species is apparently restricted to the southern two-thirds of Madagascar's eastern rainforest, with a range < 20,000 km², with severely fragmented populations, and within forest habitat that is continuing to decline in extent and/or quality. Meets IUCN (1996) criteria for Vulnerable status.

Boucardicus divei

Fischer-Piette, Blanc, Blanc & Salvat, 1993

(Figures 8, 30, 39, 60)

Boucardicus sp. 7, Emberton et al., 1996:210. Emberton, 1997:1146, 1149. Emberton et al., 1999:table 2.

Representative: MBI 376.01DR (ad).

Other specimens: MBI 373.24A (1 ad), MBI 374.07D (1 ad), MBI 375.07D (1 ad), MBI 375.07A (1 ad), MBI 376.01D (1 ad, 2 juv), MBI 376.01A (1 ad [dissected]), MBI 377.09D (4 ad), MBI 377.09A (2 ad), MBI 378.09D (1 ad), MBI 378.09A (1 ad, 3 juv), MBI 379.10D (6 ad), MBI 379.10A (3 ad, 1 juv), MBI 380.24A (1 ad [dissected]), MBI 382.26A (1 ad), MBI 388.02D (16 ad, 6 juv; AMS C.203425 [1 ad]; MNHN [1 ad]; ANSP 400824 [1 ad]), MBI 388.02A (1 ad).

Description of representative shell:

Size and Shape. Diameter 5.0 mm; height 5.5 mm. Height-diameter ratio 1.1. Spire angle 75 degrees. Whorl periphery round. Whorl shoulder round. Umbilicus before body whorl constriction 2% of shell diameter. Final umbilicus 13% of shell diameter. Whorls 4.8.

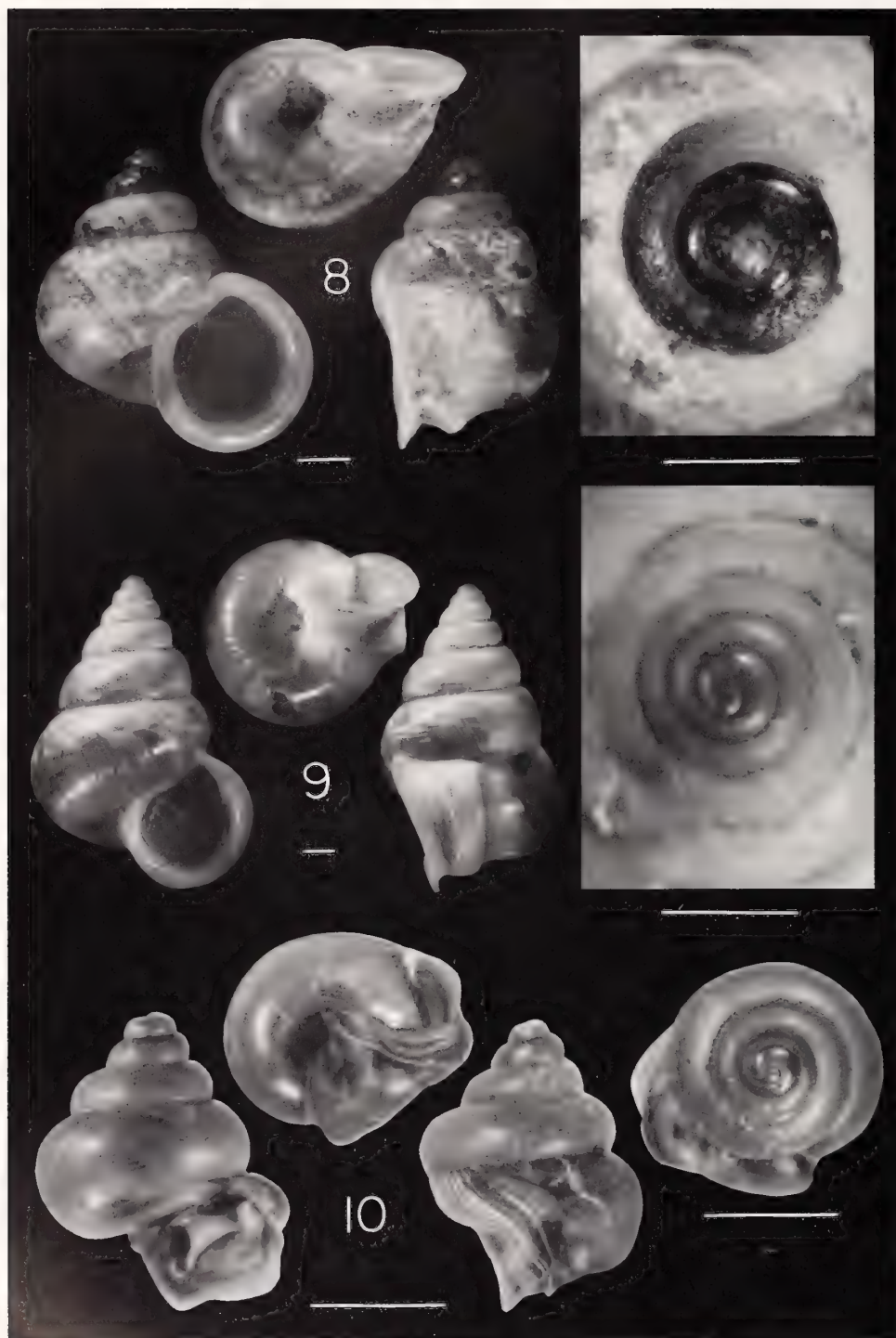
Aperture. Aperture width parallel to parietal callus 41% of shell diameter. Aperture height-width ratio (height measured perpendicular to parietal callus) 0.97. Columellar plica absent. Apertural plane inclined downward; 5 degrees from rotational axis. No apertural anal notch. No baso-columellar denticle. No basal denticle. No upper palatal denticle. Ratio of aperture plus peristome greatest width (measured parallel to or within 40 degrees of parietal-callus line) to aperture width 1.48. Aperture plus peristome greatest dimension angled outward from rotational axis 40 degrees. Ratio of aperture plus peristome greatest width to aperture plus peristome greatest height as measured perpendicular to width line 1.09. No peristome baso-palatal indentation. No peristome upper curl forward extension. Inner, second peristome absent.

Apex. Embryonic whorls 2.1. Embryonic sculpture smooth then slightly granular. First whorl diameter 0.73 mm. First three whorls diameter 2.10 mm.

Sculpture on Last Tenth of Penultimate Whorl. Transverse ribs 9; rib height less than 0.05% of shell diameter. No complete spiral grooves between sutures. No short spiral grooves between sutures. Seven spiral ridges between sutures; spiral ridges 1.00 mm high; spiral ridges moderately wavy. No spiral lines of punctae between sutures. No herringbone sculpture; no honeycomb sculpture.

Pre-Apertural Morphology. Body whorl constricted 0.1 whorl before aperture; constricting by less than 0.5% of whorl diameter. Body whorl sculpture not diminishing before constriction. Post-constriction body whorl swollen by 0% of constriction diameter. Secondary body whorl constriction present; swelling after secondary constriction enlarged by 0% of diameter of first constriction. Transverse ribs on post-constrictional swelling numbering 17 in 0.1 whorl; rib height 0.4% of shell diameter; ribs slanting forward; 10 degrees.

Color. Basic color light yellow-brown. Apex dark red-brown. One spiral color band; color white. Pre-apertural constriction white. Peristome (excluding periostracum) white.



Explanation of Figures 8–10

Shells of Mahermana-Ilapiry-Vasiha *Boucardicus*. Figure 8. *Boucardicus divei* Fischer-Piette, Blanc, Blanc & Salvat, 1993, representative from Mount Mahermana. Figure 9. *Boucardicus culminans* Fischer-Piette, Blanc, Blanc & Salvat, 1993, representative from Mount Mahermana. Figure 10. *Boucardicus tridentatus* Emberton & Pearce, sp. nov., holotype. All scale bars 1 mm.

Shell variation: Among the six adults from station MBI-379, shell height ranges from 4.4 to 5.1 mm. This is greater than the height variation among the 19 adults from MBI-388.

Description of reproductive characters (MBI 376.01A: 1 female; MBI 380.24A: 1 male): Penis length 3.0 mm, 0.6 shell diameter. Penial papilla-ejaculatory-pore position dorsal. Penial dorsal papilla terminal, little protrusion, ventrally directed. Penis terminal swelling undetectable, terminal-bulb width 1.0 pre-bulb width. Penial gland present. Penial-gland length 1.4 penis pre-terminal-bulb width. Penial-gland position proximal, its center 0.3 along the penis length from its base. Penial-gland dorso-ventral attachment position dorsal. Penial-gland free lobe direction undetectable. Base of FPSC (fertilization pouch-seminal receptacle complex) broad-based, then with narrow, subapical extension. Ducted gland on base of FPSC present. Muscular funnel within body of FPSC absent. Body-and-tube shape of FPSC: upper body straight, apex-plus-tube a rounded, up-pointed, backward "S."

Local distribution: On all three mountains, from 100 to 860 m elevation. Originally described from the Anosy chain (north of Mt. Vasiha), at about 1000 m elevation (Fischer-Piette et al., 1993). Also found at 800 m on Andohahela, Anosy chain (Emberton, in press: MBI 800), but nowhere else. Thus, apparently restricted to the Anosy and Vohimena chains, with a range extent well under 5000 km², with severely fragmented populations, and within forest habitat that is continuing to decline in extent and/or quality. Meets IUCN (1996) criteria for Endangered status.

Boucardicus culminans

Fischer-Piette, Blanc, Blanc & Salvat, 1993

(Figures 9, 40, 52, 54, 62)

Boucardicus culminans Fischer-Piette et al., 1993, Emberton, 1996:735.

Boucardicus sp. 8, Emberton et al., 1996:210. Emberton, 1997:1147. Emberton et al., in press:table 2.

Representative: MBI 376.02DR (ad).

Other specimens: MBI 374.08D (1 juv), MBI 376.02D (2 juv; AMS C. 203426 [1 ad fragment]) MBI 390.06A (2 ad [2 dissected]).

Description of representative shell:

Size and Shape. Diameter 6.5 mm; height 9.1 mm. Height-diameter ratio 1.4. Spire angle 55 degrees. Whorl periphery round. Whorl shoulder round. Umbilicus before body whorl constriction 2% of shell diameter. Final umbilicus 12% of shell diameter. Whorls 7.0.

Aperture. Aperture width parallel to parietal callus 34% of shell diameter. Aperture height-width ratio (height measured perpendicular to parietal callus) 1.09. Colu-

mellar plica absent. Apertural plane inclined downward; 15 degrees from rotational axis. No apertural anal notch. No baso-columellar denticle. No basal denticle. No upper palatal denticle. Ratio of aperture plus peristome greatest width (measured parallel to or within 40 degrees of parietal-callus line) to aperture width 1.45. Aperture plus peristome greatest dimension angled outward from rotational axis 35 degrees. Ratio of aperture plus peristome greatest width to aperture plus peristome greatest height as measured perpendicular to width line 1.26. No peristome baso-palatal indentation. No peristome upper curl forward extension. Inner, second peristome absent.

Apex. Embryonic whorls 1.9. Embryonic sculpture smooth then slightly granular. First whorl diameter 0.60 mm. First three whorls diameter 1.60 mm.

Sculpture on Last Tenth of Penultimate Whorl. Transverse ribs 20; rib height 0.5% of shell diameter. No complete spiral grooves between sutures. No short spiral grooves between sutures. No spiral ridges between sutures. No spiral lines of punctae between sutures. No her-ringbone sculpture; no honeycomb sculpture.

Pre-Apertural Morphology. Body whorl constricted 0.1 whorl before aperture; constricting by 1% of whorl diameter. Body whorl sculpture diminishes 80% before constriction. Post-constriction body whorl swollen by 18% of constriction diameter. No secondary body whorl constriction. Transverse ribs on post-constrictional swelling numbering 16 in 0.1 whorl; rib height 0.2% of shell diameter; ribs not slanted.

Color. Basic color light yellow-brown. Apex light yellow-brown. No spiral color bands. Pre-apertural constriction yellow-white. Peristome (excluding periostracum) yellow-white.

Description of reproductive characters (MBI 390.06A:

1 male, 1 female): Penis length 9.8 mm, 1.5 shell diameter. Penial papilla-ejaculatory-pore position ventral. Penis terminal swelling conspicuous, terminal-bulb width 1.3 pre-bulb width. Penial gland present. Penial-gland length 2.3 penis pre-terminal-bulb width. Penial-gland position central, its center 0.6 along the penis length from its base. Penial-gland attachment position ventral. Penial-gland free lobe direction left. Base of FPSC (fertilization pouch-seminal receptacle complex) broad-based, simple. Ducted gland on base of FPSC absent. Muscular funnel within body of FPSC present. Body-and-tube shape of FPSC: upper body straight, apex-plus-tube a rounded, up-pointed, backward "S."

Distribution: In our samples, it occurred only on Mt. Mahermana from 100 to 300 m elevation. Also reported (Emberton, in press) from Mounts Mahermana and Varabe (Vohimena Chain); from Col Beampingaratra (Anosy Chain); and 40 km east of Midongy (MBI 1445, 1448, 1499, 1458, 1372). Fischer-Piette et al. (1993) described *Boucardicus culminans* from four shells from an Anosy-Chain summit at 1900 m and from a juvenile shell col-

lected in 1950 by Millot at "Ivohibe," a locality which Fischer-Piette et al. (1993) considered to be near Andringitra. Although their description gives the range of *B. culminans* as "Madagascar Sud-Est," their range map shows a third, uncited locality in the far northeast at Marojejy. We have collected extensively in the Andringitra area and on Marojejy and environs without finding *B. culminans* (Emberton, in press). We conclude that the Marojejy locality is spurious and that the "Ivohibe" juvenile shell was either misidentified or was actually from Varabe, Vohimena Chain, which lies very near the road north of Fort Dauphin (so might well have been visited by Millot) and is referred to by locals as "Ivohibe." Thus it seems likely that this species ranges from the northern Vohimena and Anosy chains north to the Midongy area. This would give it a range of well under 5000 km², with severely fragmented populations in forest habitat that is continuing to decline in extent and/or quality of habitat. *B. culminans* therefore meets IUCN (1996) criteria for Endangered status.

Boucardicus tridentatus Emberton & Pearce,
sp. nov.

(Figures 10, 11, 41, 63)

Boucardicus sp. 9, Emberton et al., 1996:209, 210. Emberton, 1997:1146, 1149. Emberton et al., in press:table 2.

Holotype: USNM 860780 (ex MBI 385.02DH, adult shell).

Paratypes: MBI 373.14DP (1 juv), MBI 373.14AP (2 juv), MBI 374.09DP (1 juv), MBI 375.08DP (1 ad, 1 juv), MBI 375.08AP (2 ad), MBI 376.06DP (1 ad, 1 juv), MBI 376.06AP (2 ad), MBI 378.19AP (1 juv), MBI 379.11DP (2 ad), MBI 379.11AP (2 ad, 1 juv), MBI 380.09DP (1 ad), MBI 382.27AP (2 ad, 1 juv), MBI 383.06DP (1 ad), MBI 383.06AP (4 ad), MBI 384.10DP (1 ad), MBI 384.10AP (1 ad), MBI 385.02DP (10 ad; AMS C.203427 [1 ad]; MNHN [1 ad]; ANSP 400825 [1 ad]), MBI 385.02AP (11 ad [2 dissected], 4 juv), MBI 386.14AP (1 juv), MBI 387.04DP (6 ad, 2 juv), MBI 387.04AP (4 ad, 1 juv).

Type locality: Madagascar: Tulear Province: northwest of Fort Dauphin: west of village of Malio: eastsoutheast-facing valley on Mount Vasiha, 400 m elevation: latitude 24°55'25"S, longitude 46°44'45"E: primary rainforest.

Description of holotype shell:

Size and Shape. Diameter 1.8 mm; height 2.2 mm. Height-diameter ratio 1.2. Spire angle 70 degrees. Whorl periphery round. Whorl shoulder round. Umbilicus before body whorl constriction 3% of shell diameter. Final umbilicus 15% of shell diameter. Whorls 4.5.

Aperture. Aperture width parallel to parietal callus 42% of shell diameter. Aperture height-width ratio (height measured perpendicular to parietal callus) 0.67. Colu-

mellar plica absent. Apertural plane inclined downward; 35 degrees from rotational axis. No apertural anal notch. Baso-columellar denticle present; size 32% of apertural width; depth 0.20 whorl. Basal denticle present; size 20% of apertural width; depth 0.05 whorl. Upper palatal denticle present; size 33% of apertural width; depth 0.20 whorl. Ratio of aperture plus peristome greatest width (measured parallel to or within 40 degrees of parietal-callus line) to aperture width 1.42. Aperture plus peristome greatest dimension angled outward from rotational axis 55 degrees. Ratio of aperture plus peristome greatest width to aperture plus peristome greatest height as measured perpendicular to width line 1.06. Peristome baso-palatal indentation 27% of basal peristome width. No peristome upper curl forward extension. Inner, second peristome absent.

Apex. Embryonic whorls 1.8. Embryonic sculpture smooth then granular. First whorl diameter 0.37 mm. First three whorls diameter 1.05 mm.

Sculpture on Last Tenth of Penultimate Whorl. No transverse ribs. No complete spiral grooves between sutures. No short spiral grooves between sutures. No spiral ridges between sutures. No spiral lines of punctae between sutures. Ten herringbones; no honeycomb sculpture.

Pre-Apertural Morphology. Body whorl constricted 0.4 whorl before aperture; constricting by 8% of whorl diameter. Body whorl sculpture diminishes 50% before constriction. Post-constriction body whorl swollen by 36% of constriction diameter. Secondary body whorl constriction present; swelling after secondary constriction enlarged by 91% of diameter of first constriction. Transverse ribs on post-constrictional swelling numbering 14 in 0.1 whorl; rib height 1.7% of shell diameter; ribs slanting forward; 90 degrees.

Color. Basic color brown. Apex brown. No spiral color bands. Pre-apertural constriction brown. Peristome (excluding periostracum) brown.

Shell variation: No conspicuous variation in size or shape.

Shell comparisons: Most similar to *Boucardicus andringitrae* Fischer-Piette, Blanc, Blanc & Salvat, 1993, but smaller, taller, and with very different apertural and preapertural morphology.

Description of reproductive characters (MBI 385.02AP: 1 male, 1 female):

Penis length 1.3 mm, 0.7 shell diameter. Penial papilla-ejaculatory-pore position dorsal. Penial dorsal papilla terminal, strong protrusion, anteriorly directed. Penis terminal swelling slight, terminal-bulb width 1.1 pre-bulb width. Penial gland absent. Base of FPSC (fertilization pouch-seminal receptacle complex) broad-based, with fingerlike basal appendage. Ducted gland on base of FPSC absent. Body-and-tube

shape of FPSC: upper body bent right and downward, apex-plus-tube an up-pointed "U."

Distribution: On all three mountains, through the full range of elevations (100–860 m). Also found on three other peaks in the Vohimena Chain (St. Louis, Vohibololo, and Esetra); in two patches of coastal forest (Ste. Luce and 2.1 km south of Manambato) east of the northern Vohimena Chain; east of Midongy; and in Manombo Reserve (23°01'S, 47°44'E); but nowhere else. Thus *Boucardicus tridentatus*'s range seems limited to the leeward rainforests from Manombo south to Pic St. Louis, and to only the southernmost Anosy Chain. This is well under 5000 km² of declining and degrading forest, within which *B. tridentatus* exists in isolated subpopulations separated by cleared land. Thus this is an Endangered species under IUCN (1996) criteria.

Comments: During shell ontogeny, the columellar denticle starts formation low, simultaneous with the formation of the palatal denticle, and before formation of the basal denticle (Figure 11).

Etymology: For the three (*L. tri*-) teeth (*L. dentatus*) in the aperture.

Boucardicus rakotoarisoni Emberton & Pearce,
sp. nov.

(Figures 12, 27, 42, 43, 64)

Boucardicus n. sp. 27, in part, Emberton, 1996:735.

Boucardicus sp. 10, Emberton et al., 1996:210. Emberton, 1997:1147. Emberton et al., 1999:table 2.

Holotype: USNM 860781 (ex MBI 373.02DH, adult shell).

Paratypes: MBI 373.02AP (1 ad [dissected]), MBI 374.10DP (1 ad), MBI 374.10AP (2 ad [2 dissected]), MBI 382.09DP (0; AMS C.203428 [1 ad]).

Type locality: Madagascar: Tulear Province: north of Fort Dauphin: northeast of village of Esetra: summit of Mount Mahermana, 340 m elevation: latitude 24°26'12"S, longitude 47°13'13"E: primary rainforest.

Description of holotype shell:

Size and Shape. Diameter 1.8 mm; height 2.2 mm. Height-diameter ratio 1.2. Spire angle 80 degrees. Whorl periphery round. Whorl shoulder round. Umbilicus before body whorl constriction 6% of shell diameter. Final umbilicus 13% of shell diameter. Whorls 4.2.

Aperture. Aperture width parallel to parietal callus 32% of shell diameter. Aperture height-width ratio (height measured perpendicular to parietal callus) 1.17. Columellar plica absent. Apertural plane inclined downward; 40 degrees from rotational axis. No apertural anal notch. Baso-columellar denticle present; size 15% of apertural width; depth 0.10 whorl. No basal denticle. No upper palatal denticle. Ratio of aperture plus peristome greatest

width (measured parallel to or within 40 degrees of parietal-callus line) to aperture width 1.63. Aperture plus peristome greatest dimension angled outward from rotational axis 45 degrees. Ratio of aperture plus peristome greatest width to aperture plus peristome greatest height as measured perpendicular to width line 1.03. Peristome baso-palatal indentation 55% of basal peristome width. No peristome upper curl forward extension. Inner, second peristome absent.

Apex. Embryonic whorls 2.0. Embryonic sculpture smooth. First whorl diameter 0.42 mm. First three whorls diameter 1.24 mm.

Sculpture on Last Tenth of Penultimate Whorl. No transverse ribs. No complete spiral grooves between sutures. Eighteen short spiral grooves between sutures; short spiral grooves 0.06 mm long. No spiral ridges between sutures. No spiral lines of punctae between sutures. No herringbone sculpture; no honeycomb sculpture.

Pre-Apertural Morphology. Body whorl constricted 0.4 whorl before aperture; constricting by 22% of whorl diameter. Body whorl sculpture diminishes 70% before constriction. Post-constriction body whorl swollen by 24% of constriction diameter. Secondary body whorl constriction present; swelling after secondary constriction enlarged by 57% of diameter of first constriction. Transverse ribs on post-constrictional swelling numbering 9 in 0.1 whorl; rib height 1.1% of shell diameter; ribs not slanted.

Color. Basic color brown. Apex brown. No spiral color bands. Pre-apertural constriction brown. Peristome (excluding periostracum) brown.

Shell variation: The adult from station MBI-374 is much smaller than the holotype: height 2.0 mm.

Shell comparisons: Most similar to *Boucardicus clarea* Emberton, 1994, which however lacks the sculpture and the great preapertural swelling of this species, and which has a much more trilobed peristome.

Description of reproductive characters (MBI 373.02AP: 1 female; MBI 374.10AP: 1 male, 1 female): Penis length 1.4 mm, 0.8 shell diameter. Penial papilla-ejaculatory-pore position dorsal. Penial dorsal papilla absent. Penis terminal swelling conspicuous, terminal-bulb width 1.4 pre-bulb width. Penial gland absent. Base of FPSC (fertilization pouch-seminal receptacle complex) narrow-based, unlobed. Ducted gland on base of FPSC present. Muscular funnel within body of FPSC absent. Body-and-tube shape of FPSC: upper mid-body folded left, apex-plus-tube a squashed, backward "S."

Distribution: Found on Mts. Mahermana and Vasiha, from 300 to 860 m elevation. Also reported (Emberton, in press) from Mt. Teloboko, near Mahermana; from Andohahela (400–1100 m) and Beampingaratra in the Anosy Chain (380–500 m); and from Mount Ramabeafo (300–560 m), which runs between the southern Anosy and Vohimena Chains; but nowhere else. Thus a species



Explanation of Figures 11–13

Shells of Mahermana-Ilapiry-vasiha *Boucardicus*. Figure 11. *Boucardicus tridentatus* Emberton & Pearce, sp. nov., juvenile paratype. Figure 12. *Boucardicus rakotoarisoni* Emberton & Pearce, sp. nov., holotype. Figure 13. *Boucardicus simplex* Emberton & Pearce, sp. nov., holotype. All scale bars 1 mm.

of higher elevations (300+ m) that ranges throughout the Anosy Chain with extensions into the northern Vohimana Chain and toward but not into the southern Vohimana Chain. Thus *Boucardicus rakotoarisoni* occurs in fragmented populations within less than 1000 km² of declining forest, so meets criteria (IUCN, 1996) for Endangered status.

Etymology: For Jean Marcel Rakotoarison of the Rano-mafana National Park Project, former student and skilled associate in both field and lab, who has collected extensively on Andohahela.

Boucardicus simplex Emberton & Pearce, sp. nov.

(Figure 13)

Boucardicus sp. 11, Emberton et al., 1996:210. Emberton, 1997:1146, 1149. Emberton et al., 1999:table 2.

Holotype: USNM 860782 (ex MBI 377.01DH, adult shell).

Paratypes: MBI 377.01DP (2 ad, 3 juv; AMS C.203429 [1 ad]; MNHN [1 ad]; ANSP 400826 [1 ad]), 378.10DP (1 ad), MBI 379.12DP (2 juv).

Type locality: Madagascar: Tulear Province: north of Fort Dauphin: west of village of Mahialambo: summit of Mount Ilapiry, 540 m elevation: latitude 24°51'40"S, longitude 47°00'20"E: primary rainforest.

Description of holotype shell:

Size and Shape. Diameter 3.6 mm; height 4.2 mm. Height-diameter ratio 1.2. Spire angle 65 degrees. Whorl periphery round. Whorl shoulder round. Umbilicus before body whorl constriction 4% of shell diameter. Final umbilicus 6% of shell diameter. Whorls 5.6.

Aperture. Aperture width parallel to parietal callus 42% of shell diameter. Aperture height-width ratio (height measured perpendicular to parietal callus) 0.95. Columellar plica absent. Apertural plane inclined downward; 10 degrees from rotational axis. No apertural anal notch. No baso-columellar denticle. No basal denticle. No upper palatal denticle. Ratio of aperture plus peristome greatest width (measured parallel to or within 40 degrees of parietal-callus line) to aperture width 1.18. Aperture plus peristome greatest dimension angled outward from rotational axis 35 degrees. Ratio of aperture plus peristome greatest width to aperture plus peristome greatest height as measured perpendicular to width line 0.90. No peristome baso-palatal indentation. No peristome upper curl forward extension. Inner, second peristome absent.

Apex. Embryonic whorls 1.5. Embryonic sculpture smooth. First whorl diameter 0.45 mm. First three whorls diameter 1.13 mm.

Sculpture on Last Tenth of Penultimate Whorl. Transverse ribs 24; rib height less than 0.05% of shell diameter. No complete spiral grooves between sutures. No short spiral grooves between sutures. No spiral ridges between

sutures. Seventeen spiral lines of punctae between sutures; spiral lines of punctae numbering 24 per 0.1 whorl. No herringbone sculpture; no honeycomb sculpture.

Pre-Apertural Morphology. Body whorl constricted 0.1 whorl before aperture; constricting by 1% of whorl diameter. Body whorl sculpture not diminishing before constriction. Post-constriction body whorl swollen by 1% of constriction diameter. No secondary body whorl constriction. Transverse ribs on post-constrictional swelling numbering 18 in 0.1 whorl; rib height less than 0.05% of shell diameter; ribs not slanted.

Color. Basic color yellow. Apex yellow. No spiral color bands. Pre-apertural constriction red-brown. Peristome (excluding periostracum) white.

Shell variation: The five adult dry shells from MBI-377 range in height from 3.0 to 4.1 mm.

Shell comparisons: Much smaller and more acutely spired than *Boucardicus soulaianus* Fischer-Piette, Blanc, Blanc & Salvat, 1993. Smaller aperture and more acutely spired than *B. peani* Fischer-Piette, Blanc, Blanc & Salvat, 1993.

Reproductive characters: Unknown.

Distribution: Found only on Mt. Ilapiry, from only 400 to 540 m elevation. Not known from any other localities (Emberton, in press). A Critically Endangered species, by IUCN (1996) criteria, because its extent of occurrence is much less than 100 km², it is known from just a single location, and slash-and-burn agriculture is continually destroying its habitat.

Etymology: For the relatively simple (*L. simplex*) shape of the shell.

Boucardicus fortistriatus Emberton & Pearce, sp. nov.

(Figure 14)

Boucardicus sp. 12, Emberton et al., 1996:210. Emberton, 1997:1147. Emberton et al., 1999:table 2.

Holotype: USNM 860783 (ex MBI 382.02DH, adult shell).

Paratypes: MBI 382.02DP (0; AMS C.203430 [1 ad]).

Type locality: Madagascar: Tulear Province: northwest of Fort Dauphin: west of village of Malio: local summit of Mount Vasiha, south of main summit, 860 m elevation: latitude 24°55'18"S, longitude 46°44'19"E: primary rainforest.

Description of holotype shell:

Size and Shape. Diameter 2.1 mm; height 2.3 mm. Height-diameter ratio 1.1. Spire angle 80 degrees. Whorl periphery round. Whorl shoulder round. Umbilicus before body whorl constriction 2% of shell diameter. Final umbilicus 12% of shell diameter. Whorls 4.4.



Explanation of Figures 14–16

Shells of Mahermana-Ilapiry-Vasiha *Boucardicus*. Figure 14. *Boucardicus fortistriatus* Emberton & Pearce, sp. nov., holotype. Figure 15. *Boucardicus mahermanae* Emberton & Pearce, sp. nov., holotype. Figure 16. *Boucardicus carylae* Emberton & Pearce, sp. nov., holotype. All scale bars 1 mm.

Aperture. Aperture width parallel to parietal callus 38% of shell diameter. Aperture height-width ratio (height measured perpendicular to parietal callus) 0.89. Columellar plica absent. Apertural plane inclined downward; 30 degrees from rotational axis. No apertural anal notch. No baso-columellar denticle. No basal denticle. No upper palatal denticle. Ratio of aperture plus peristome greatest width (measured parallel to or within 40 degrees of parietal-callus line) to aperture width 1.44. Aperture plus peristome greatest dimension angled outward from rotational axis 40 degrees. Ratio of aperture plus peristome greatest width to aperture plus peristome greatest height as measured perpendicular to width line 1.31. Peristome baso-palatal indentation 20% of basal peristome width. No peristome upper curl forward extension. Inner, second peristome absent.

Apex. Embryonic whorls 1.6. Embryonic sculpture smooth. First whorl diameter 0.40 mm. First three whorls diameter 1.28 mm.

Sculpture on Last Tenth of Penultimate Whorl. No transverse ribs. No complete spiral grooves between sutures. No short spiral grooves between sutures. Nineteen spiral ridges between sutures; spiral ridges 1.00 mm high; spiral ridges not wavy. No spiral lines of punctae between sutures. No herringbone sculpture; no honeycomb sculpture.

Pre-Apertural Morphology. Body whorl constricted 0.2 whorl before aperture; constricting by 13% of whorl diameter. Body whorl sculpture not diminishing before constriction. Post-constriction body whorl swollen by 22% of constriction diameter. Secondary body whorl constriction present; swelling after secondary constriction enlarged by 30% of diameter of first constriction. Transverse ribs on post-constrictional swelling numbering 11 in 0.1 whorl; rib height 1.0% of shell diameter; ribs slanting backward; 10 degrees.

Color. Basic color brown-red. Apex brown-red. No spiral color bands. Pre-apertural constriction brown-red. Peristome (excluding periostracum) brown-red.

Shell comparisons: Unique for its strong spiral sculpture and compact, simple shape.

Reproductive characters: Unknown.

Distribution: Known only from Mt. Vasiha, on a local summit of 860 m elevation. Not known from any other localities (Emberton, in press). Like the above species, *Boucardicus fortistriatus* sp. nov. is Critically Endangered by IUCN (1996) criteria, because its extent of occurrence is much less than 100 km², it is known from just a single location, and slash-and-burn agriculture is continually eroding its habitat.

Etymology: For the sculpture of strong (*L. forti-*) spiral grooves (*L. striatus*).

Boucardicus mahermanae Emberton & Pearce,
sp. nov.

(Figures 15, 44, 65)

Boucardicus sp. 13, Emberton et al., 1996:210. Emberton, 1997:1146, 1149. Emberton et al., 1999:table 2.

Holotype: USNM 860784 (ex MBI 373.03DH, adult shell).

Paratypes: MBI 373.03DP (1 juv; AMS C.203431 [1 ad]), MBI 373.03AP (7 ad [2 dissected]), MBI 374.24AP (3 ad), MBI 376.21AP (1 ad), MBI 380.25AP (1 juv).

Type locality: Madagascar: Tulear Province: north of Fort Dauphin: northeast of village of Esetra: summit of Mount Mahermana, 340 m elevation: latitude 24°26'12"S, longitude 47°13'13"E: primary rainforest.

Description of holotype shell:

Size and Shape. Diameter 3.2 mm; height 3.0 mm. Height-diameter ratio 0.9. Spire angle 70 degrees. Whorl periphery round. Whorl shoulder round. Umbilicus before body whorl constriction 4% of shell diameter. Final umbilicus 19% of shell diameter. Whorls 4.2.

Aperture. Aperture width parallel to parietal callus 28% of shell diameter. Aperture height-width ratio (height measured perpendicular to parietal callus) 0.96. Columellar plica absent. Apertural plane inclined upward; 5 degrees from rotational axis. Apertural anal notch 7% of apertural width. No baso-columellar denticle. No basal denticle. No upper palatal denticle. Ratio of aperture plus peristome greatest width (measured parallel to or within 40 degrees of parietal-callus line) to aperture width 2.11. Aperture plus peristome greatest dimension angled outward from rotational axis 30 degrees. Ratio of aperture plus peristome greatest width to aperture plus peristome greatest height as measured perpendicular to width line 1.29. Peristome baso-palatal indentation 44% of basal peristome width. Peristome upper curl extends forward 100% of upper peristome width. Inner, second peristome present, projecting more than 0.01 whorl.

Apex. Embryonic whorls 1.9. Embryonic sculpture smooth. First whorl diameter 0.63 mm. First three whorls diameter 1.73 mm.

Sculpture on Last Tenth of Penultimate Whorl. No transverse ribs. No complete spiral grooves between sutures. No short spiral grooves between sutures. No spiral ridges between sutures. No spiral lines of punctae between sutures. No herringbone sculpture; no honeycomb sculpture.

Pre-Apertural Morphology. Body whorl constricted 0.5 whorl before aperture; constricting by 12% of whorl diameter. Body whorl sculpture not diminishing before constriction. Post-constriction body whorl swollen by 12% of constriction diameter. Secondary body whorl constriction present; swelling after secondary constriction enlarged by 27% of diameter of first constriction. Transverse ribs on

post-constrictional swelling numbering 12 in 0.1 whorl; rib height 1.6% of shell diameter; ribs slanting forward; 30 degrees.

Color. Basic color brown-red. Apex brown-red. Two spiral color bands; color white. Pre-apertural constriction brown-red. Peristome (excluding periostracum) red-brown and white.

Shell comparisons: Most similar to *Boucardicus andringitrae* Fischer-Piette, Blanc, Blanc & Salvat, 1993, but without severe swellings and apertural dentition, and with a robust upper forward extension of the peristome.

Description of reproductive characters (MBI 373.03AP: 1 male, 1 female): Penis length 2.7 mm, 0.8 shell diameter. Penial papilla-ejaculatory-pore position dorsal. Penial dorsal papilla terminal, weak to no protrusion beyond tip of penis, anteriorly directed. Penis terminal swelling slight, terminal-bulb width 1.2 pre-bulb width. Penial gland present. Penial-gland length 1.4 penis pre-terminal-bulb width. Penial-gland position proximal, its center 0.4 along the penis length from its base. Penial-gland attachment position ventral. Penial-gland free lobe direction left. Base of FPSC (fertilization pouch-seminal receptacle complex) narrow-based, with two ovate apical lobes. Ducted gland on base of FPSC absent. Body-and-tube shape of FPSC: upper mid-body folded left, apex-plus-tube a squashed, backward "S."

Distribution: On both Vohimena-Chain mountains (Maherana and Ilapiry), from 100 to 340 m elevation. Also found in two patches of coastal forest just east of the Vohimena Chain (Ste. Luce and 4.6 km south of Manambato), and found in the near-coastal forest (elevation ca. 50 m) of Manombo, but nowhere else (Emberton, in press). Thus, restricted to lowland coastal forest between Manombo (some 33 km south of Farafangana) and Mount Ilapiry. This forest is continually diminishing and/or degrading and extends much less than 5000 km². *Boucardicus maheranae* sp. nov. is severely fragmented into subpopulations surviving in remnant patches of forest. By these criteria, it is an Endangered species (IUCN, 1996).

Etymology: For Mount Maherana, northern Vohimena Chain.

Boucardicus carylae Emberton & Pearce, sp. nov.
(Figures 16, 45, 66)

Boucardicus sp. 14, Emberton et al., 1996:210. Emberton, 1997:1147. Emberton et al., 1999:table 2.

Holotype: USNM 860785 (ex MBI 377.02DH, adult shell).

Paratypes: MBI 377.02DP (1 ad, 2 juv; AMS C.203432 [1 ad]), MBI 377.02AP (6 ad), MBI 378.20AP (7 ad [1 dissected]), MBI 379.34AP (1 ad, 1 juv), MBI 382.10DP (1 ad), MBI 382.10AP (2 ad [1 dissected]).

Type locality: Madagascar: Tulear Province: north of Fort Dauphin: west of village of Mahialambo: summit of Mount Ilapiry, 540 m elevation: latitude 24°51'40"S, longitude 47°00'20"E: primary rainforest.

Description of holotype shell:

Size and Shape. Diameter 1.5 mm; height 1.7 mm. Height-diameter ratio 1.1. Spire angle 65 degrees. Whorl periphery round. Whorl shoulder round. Umbilicus before body whorl constriction 2% of shell diameter. Final umbilicus 9% of shell diameter. Whorls 4.4.

Aperture. Aperture width parallel to parietal callus 34% of shell diameter. Aperture height-width ratio (height measured perpendicular to parietal callus) 0.95. Columellar plica absent. Apertural plane inclined upward; 15 degrees from rotational axis. Apertural anal notch 7% of apertural width. No baso-columellar denticle. No basal denticle. No upper palatal denticle. Ratio of aperture plus peristome greatest width (measured parallel to or within 40 degrees of parietal-callus line) to aperture width 1.68. Aperture plus peristome greatest dimension angled outward from rotational axis 25 degrees. Ratio of aperture plus peristome greatest width to aperture plus peristome greatest height as measured perpendicular to width line 1.42. Peristome baso-palatal indentation 83% of basal peristome width. Peristome upper curl extends forward 33% of upper peristome width. Inner, second peristome present, projecting less than 0.01 whorl.

Apex. Embryonic whorls 1.8. Embryonic sculpture smooth. First whorl diameter 0.29 mm. First three whorls diameter 0.78 mm.

Sculpture on Last Tenth of Penultimate Whorl. Transverse ribs 12; rib height 0.7% of shell diameter. No complete spiral grooves between sutures. No short spiral grooves between sutures. No spiral ridges between sutures. No spiral lines of punctae between sutures. No heringbone sculpture; no honeycomb sculpture.

Pre-Apertural Morphology. Body whorl constricted 0.1 whorl before aperture; constricting by 16% of whorl diameter. Body whorl sculpture diminishes 50% before constriction. Post-constriction body whorl swollen by 32% of constriction diameter. No secondary body whorl constriction. Transverse ribs on post-constrictional swelling numbering 9 in 0.1 whorl; rib height 0.7% of shell diameter; ribs not slanted.

Color. Basic color yellow-brown. Apex yellow-brown. No spiral color bands. Pre-apertural constriction yellow-brown. Peristome (excluding periostracum) yellow-brown.

Shell variation: No conspicuous variation in size or shape.

Shell comparisons: Unique in its combination of ribbed overall sculpture, post-constriction swelling that is extreme and close to the aperture, and upper outer peristome that flares broadly at and adherent to the body whorl.

Description of reproductive characters (MBI 378.20AP: 1 male; MBI 382.10AP: 1 female): Penis length 0.9 mm, 0.6 shell diameter. Penial papilla-ejaculatory-pore position central. Penis terminal swelling slight, terminal-bulb width 1.1 pre-bulb width. Penial gland absent. Base of FPSC (fertilization pouch-seminal receptacle complex) narrow-based, with multiple apical lobes. Ducted gland on base of FPSC absent. Body-and-tube shape of FPSC: upper body bent right and downward, apex-plus-tube an up-pointed "U."

Distribution: Mts. Ilapiry and Vasiha, 540–860 m elevation. Also found on Andohahela, 800–1900 m; but nowhere else (Emberton, in press). Its range, therefore, seems restricted to the southern Anosy and Vohimena Chains, and extends less than 1000 km². Its area and quality of habitat are under continuing decline, and its distribution is severely fragmented by its apparent restriction to high elevations (500+ m). Therefore *Boucardicus carylae* sp. nov. is an Endangered species by IUCN (1996) criteria.

Etymology: For Caryl Hesterman, in grateful recognition of her former service as Secretary-Treasurer of the Molluscan Biodiversity Institute.

Boucardicus magnilobatus Emberton & Pearce,
sp. nov.

(Figure 17)

Boucardicus n. sp. 27, in part, Emberton, 1996:735.

Boucardicus sp. 15, Emberton et al., 1996:210. Emberton, 1997:1147. Emberton et al., 1999:table 2.

Holotype: USNM 860786 (ex MBI 378.01DH, adult shell).

Paratypes: None.

Type locality: Madagascar: Tulear Province: north of Fort Dauphin: west of village of Mahialambo: east-facing ridge of Mount Ilapiry, 500 m elevation: latitude 24°51'33"S, longitude 47°00'27"E: primary rainforest.

Description of holotype shell:

Size and Shape. Diameter 2.1 mm; height 3.0 mm. Height-diameter ratio 1.4. Spire angle 70 degrees. Whorl periphery round. Whorl shoulder round. Umbilicus before body whorl constriction 3% of shell diameter. Final umbilicus 10% of shell diameter. Whorls 4.3.

Aperture. Aperture width parallel to parietal callus 35% of shell diameter. Aperture height-width ratio (height measured perpendicular to parietal callus) 1.19. Columellar plica absent. Apertural plane inclined downward; 50 degrees from rotational axis. No apertural anal notch. No baso-columellar denticle. No basal denticle. No upper palatal denticle. Ratio of aperture plus peristome greatest width (measured parallel to or within 40 degrees of parietal-callus line) to aperture width 1.21. Aperture plus

peristome greatest dimension angled outward from rotational axis 90 degrees. Ratio of aperture plus peristome greatest width to aperture plus peristome greatest height as measured perpendicular to width line 0.82. Peristome baso-palatal indentation 43% of basal peristome width. No peristome upper curl forward extension. Inner, second peristome present, projecting less than 0.01 whorl.

Apex. Embryonic whorls 1.7. Embryonic sculpture smooth. First whorl diameter 0.56 mm. First three whorls diameter 1.54 mm.

Sculpture on Last Tenth of Penultimate Whorl. No transverse ribs. No complete spiral grooves between sutures. No short spiral grooves between sutures. No spiral ridges between sutures. No spiral lines of punctae between sutures. No herringbone sculpture; no honeycomb sculpture.

Pre-Apertural Morphology. Body whorl constricted 0.6 whorl before aperture; constricting by 22% of whorl diameter. Body whorl sculpture not diminishing before constriction. Post-constriction body whorl swollen by 64% of constriction diameter. Secondary body whorl constriction present; swelling after secondary constriction enlarged by 100% of diameter of first constriction. Transverse ribs on post-constrictional swelling numbering 9 in 0.1 whorl; rib height 1.9% of shell diameter; ribs slanting forward; 50 degrees.

Color. Basic color brown. Apex brown. No spiral color bands. Pre-apertural constriction brown. Peristome (excluding periostracum) brown.

Shell comparisons: Most similar to *Boucardicus seguini* Fischer-Piette, Blanc, Blanc & Salvat, 1993, but with a much earlier preapertural constriction of the body whorl, a greater preapertural swelling, and a more triangular aperture.

Reproductive characters: Unknown.

Distribution: Mt. Ilapiry at 500 m elevation. Emberton (in press) also gives localities from Andohahela (430–1400 m), Col Beampingaratra (600–800 m), and Mt. Ramabeafo (580–700 m). Thus with a range in the Anosy and southern Vohimena Chains. An Endangered species by IUCN (1996) criteria because of its small range (< 1000 km²), decline in area and quality of habitat, and extreme fragmentation into high-elevation "islands" of forest.

Etymology: For the large (*L. magni*-) lobelike preapertural swelling (*L. lobatus*) of the body whorl.

Boucardicus fidimananai Emberton & Pearce,
sp. nov.

(Figure 18)

Boucardicus sp. 16, Emberton et al., 1996:210. Emberton, 1997:1147. Emberton et al., 1999:table 2.



Explanation of Figures 17–19

Shells of Mahermama-Ilapiry-Vasiha *Boucardicus*. Figure 17. *Boucardicus magnilobatus* Emberton & Pearce, sp. nov., holotype. Figure 18. *Boucardicus fidimananai* Emberton & Pearce, sp. nov., holotype. Figure 19. *Boucardicus randalanai* Emberton & Pearce, sp. nov., holotype. All scale bars 1 mm.

Holotype: USNM 860787 (ex MBI 378.02DH, adult shell).

Paratypes: MBI 378.02AP (1 juv).

Type locality: Madagascar: Tulear Province: north of Fort Dauphin: west of village of Mahialambo: east-facing ridge of Mount Ilapiry, 500 m elevation: latitude 24°51'33"S, longitude 47°00'27"E: primary rainforest.

Description of holotype shell:

Size and Shape. Diameter 3.3 mm; height 3.9 mm. Height-diameter ratio 1.2. Spire angle 75 degrees. Whorl periphery round. Whorl shoulder round. Umbilicus before body whorl constriction 3% of shell diameter. Final umbilicus 12% of shell diameter. Whorls 4.5.

Aperture. Aperture width parallel to parietal callus 43% of shell diameter. Aperture height-width ratio (height measured perpendicular to parietal callus) 0.89. Columellar plica absent. Apertural plane parallel to rotational axis. No apertural anal notch. No baso-columellar denticle. No basal denticle. No upper palatal denticle. Ratio of aperture plus peristome greatest width (measured parallel to or within 40 degrees of parietal-callus line) to aperture width 1.11. Aperture plus peristome greatest dimension angled outward from rotational axis 55 degrees. Ratio of aperture plus peristome greatest width to aperture plus peristome greatest height as measured perpendicular to width line 1.14. No peristome baso-palatal indentation. No peristome upper curl forward extension. Inner, second peristome absent.

Apex. Embryonic whorls 2.0. Embryonic sculpture granular. First whorl diameter 0.65 mm. First three whorls diameter 1.91 mm.

Sculpture on Last Tenth of Penultimate Whorl. No transverse ribs. No complete spiral grooves between sutures. No short spiral grooves between sutures. No spiral ridges between sutures. No spiral lines of punctae between sutures. No herringbone sculpture; no honeycomb sculpture.

Pre-Apertural Morphology. Body whorl constricted 0.1 whorl before aperture; constricting by 2% of whorl diameter. Lack of body whorl sculpture continues into constriction. Post-constriction body whorl swollen by 9% of constriction diameter. No secondary body whorl constriction. Transverse ribs on post-constriction swelling numbering 18 in 0.1 whorl; rib height 1.8% of shell diameter; ribs slanting forward; 70 degrees.

Color. Basic color brown-red. Apex brown-red. No spiral color bands. Pre-apertural constriction brown-red.

Shell comparisons: Smaller and squatter than *Boucardicus peani* Fischer-Piette, Blanc, Blanc & Salvat, 1993, and without its spiral sculpture.

Reproductive characters: Unknown.

Local distribution: Known only from Mt. Ilapiry at 500 m elevation. Not reported from any other locality (Em-

berton, in press). Therefore a Critically Endangered species by IUCN (1996) criteria, occurring in much less than 100 km² of continually declining and degrading forest.

Etymology: For Fidimanana, able lab and field assistant, and dedicated student of malacology.

Boucardicus randalanai Emberton & Pearce,
sp. nov.

(Figure 19)

Boucardicus n. sp. 28, in part, Emberton, 1996:735.

Boucardicus sp. 17, Emberton et al., 1996:210. Emberton, 1997:1147. Emberton et al., 1999:table 2.

Holotype: USNM 860788 (ex MBI 373.04DH, adult shell).

Paratypes: MBI 373.04AP (1 juv).

Type locality: Madagascar: Tulear Province: north of Fort Dauphin: northeast of village of Esetra: summit of Mount Mahermana, 340 m elevation: latitude 24°26'12"S, longitude 47°13'13"E: primary rainforest.

Description of holotype shell:

Size and Shape. Diameter 1.4 mm; height 2.1 mm. Height-diameter ratio 1.4. Spire angle 70 degrees. Whorl periphery round. Whorl shoulder round. Umbilicus before body whorl constriction 9% of shell diameter. Final umbilicus 11% of shell diameter. Whorls 5.0.

Aperture. Aperture width parallel to parietal callus 39% of shell diameter. Aperture height-width ratio (height measured perpendicular to parietal callus) 1.00. Columellar plica absent. Apertural plane inclined downward; 5 degrees from rotational axis. No apertural anal notch. Baso-columellar denticle present; size 9% of apertural width; depth 0.00 whorl. No basal denticle. No upper palatal denticle. Ratio of aperture plus peristome greatest width (measured parallel to or within 40 degrees of parietal-callus line) to aperture width 1.36. Aperture plus peristome greatest dimension angled outward from rotational axis 50 degrees. Ratio of aperture plus peristome greatest width to aperture plus peristome greatest height as measured perpendicular to width line 1.06. Peristome baso-palatal indentation 29% of basal peristome width. No peristome upper curl forward extension. Inner, second peristome absent.

Apex. Embryonic whorls 1.9. Embryonic sculpture smooth. First whorl diameter 0.38 mm. First three whorls diameter 0.95 mm.

Sculpture on Last Tenth of Penultimate Whorl. Transverse ribs 80; rib height 0.7% of shell diameter. No complete spiral grooves between sutures. No short spiral grooves between sutures. No spiral ridges between sutures. No spiral lines of punctae between sutures. No herringbone sculpture; 28 honeycombs.

Pre-Apertural Morphology. Body whorl constricted 0.1 whorl before aperture; constricting by less than 0.5% of

whorl diameter. Body whorl sculpture not diminishing before constriction. Post-constriction body whorl swollen by 20% of constriction diameter. No secondary body whorl constriction. Transverse ribs on post-constrictional swelling numbering 9 in 0.1 whorl; rib height 0.7% of shell diameter; ribs slanting forward; 80 degrees.

Color. Basic color yellow. Apex brown. No spiral color bands. Pre-apertural constriction yellow. Peristome (excluding periostracum) yellow.

Shell comparisons: Unique in its honeycomb sculpture. Most similar, in its minute, high-spined shell, to *Boucardicus delicatus* sp. nov., from which it differs in its larger, more circular aperture.

Reproductive characters: Unknown.

Distribution: The summit of Mt. Mahermana, 340 m elevation. Also found at high elevation (530 m) on the adjacent Mt. Teloboko, but nowhere else (Emberton, in press). This species is fragmented into two isolated subpopulations that occupy < 10 km² of forest that is succumbing rapidly to logging and slash-and-burn agriculture. It meets criteria of the IUCN (1996) for Critically Endangered status.

Etymology: For Roger Randalana, former student and able associate in field and lab.

Genus *Cyathopoma* W. & H. Blanford, 1861

Cyathopoma randalana Emberton & Pearce,
sp. nov.

(Figures 20, 21, 31, 46, 67)

Cyathopoma sp. 1, Emberton et al., 1996:210. Emberton, 1997:1146, 1149.

Holotype: USNM 860789 (ex MBI 379.01DH, adult shell).

Paratypes: MBI 373.15DP (2 ad, 2 juv), MBI 373.15AP (1 ad), MBI 374.11DP (1 ad), MBI 374.11AP (1 ad), MBI 375.09DP (2 juv), MBI 375.09AP (2 ad [1 dissected], 3 juv), MBI 376.07DP (4 ad), MBI 376.07AP (3 ad [1 dissected]), MBI 377.22AP (1 ad, 1 juv), MBI 378.11DP (1 juv), MBI 379.01DP (4 ad, 1 juv; AMS C.203433 [1 ad]; MNHN [1 ad]; ANSP 400827 [1 ad]), MBI 379.01AP (3 ad), MBI 380.10DP (1 ad), MBI 383.07DP (2 ad, 1 juv), MBI 383.07AP (1 juv), MBI 391.04AP (1 ad).

Type locality: Madagascar: Tulear Province: north of Fort Dauphin: west of village of Mahialambo: SSE-facing side of Mount Ilapiry, 400 m elevation: latitude 24°51'27"S, longitude 47°00'38"E: primary rainforest.

Description of holotype shell:

Size and Shape. Shell dextral. Diameter 2.0 mm; height 2.0 mm. Height-diameter ratio 1.0. Whorls 4.3. Spire angle 85 degrees. Apex angle 90 degrees. Spire profile convexity (outward departure from a straight line tangent to

whorls n-0.5 and about the second whorl). 1% of shell diameter. Whorl periphery round. Suture depth one half whorl from aperture is 5% of shell diameter. Final umbilicus 20% of shell diameter. Coiling tightness (whorl number divided by natural logarithm of shell diameter) 6.2. Operculum concentric with five ridges of concentric thin lamellae.

Aperture. Aperture width (inside dimension, parallel to a line between the columellar and upper peristome insertions) 40% of shell diameter. Aperture height-width ratio (inside dimension, height measured to and perpendicular to a line between the columellar and upper peristome insertions) 0.91. Distance between columellar and upper peristome insertions is 44% of aperture width. Penultimate whorl not projecting into body whorl. Columella not truncate. Columellar plica absent. Columella not reflected. Apertural plane inclined downward; 5 degrees from rotational axis. Aperture shape circular, outer aperture with a slightly forwardly projecting curl at its baso-columellar edge. Peristome reflected; second, internal peristome present, projecting more than 0.01 whorl. Ratio of aperture width including peristome to aperture width excluding peristome 1.3. Change in growth direction of body whorl; occurs 0.2 whorls behind aperture. Apertural dentition absent.

Apex. Embryonic whorls 1.7; diameter 0.6 mm. First whorl diameter 0.4 mm. First two whorls diameter 0.7 mm. Embryonic whorls smooth.

Post-Embryonic Shell Sculpture and Color. Post-embryonic shell with extremely fine, crowded transverse grooves; upper suture canaliculate by a ridge of periostracum only; top of whorl shoulder with transverse grooves only, then between outer edge of whorl shoulder and the lower suture are five strong spiral ridges. Spiral ridge sculpture continues on shell base and into umbilicus and is unchanged at end of growth near aperture. Basic shell color white.

Shell variation: There is great variation in size, both within and among populations. Figures 20 and 21 contrast a small specimen (Figure 20) with a large (Figure 21; note difference in scale bars).

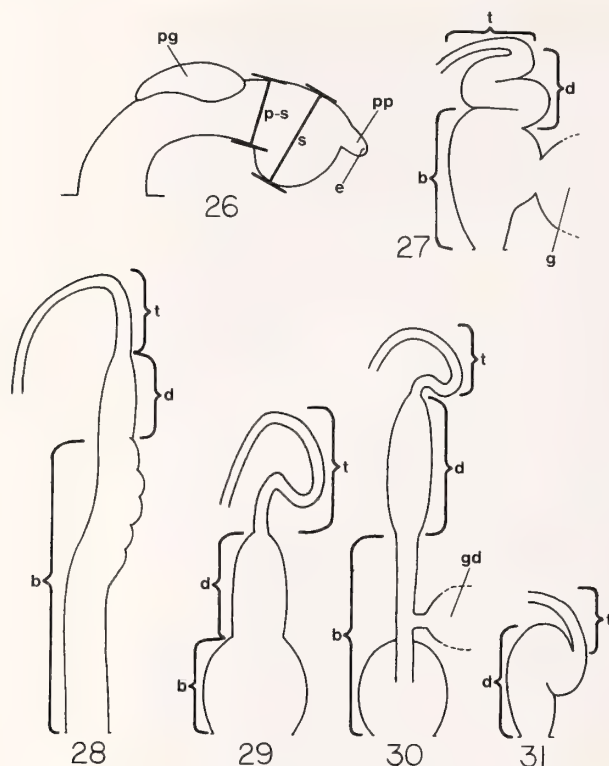
Shell comparisons: Most similar to *Cyathopoma filocinctum* Benson, 1851, but much smaller for the same number of whorls.

Description of reproductive characters (MBI 375.09AP: 1 female; MBI 376.07AP: 1 male): Penis length 1.2 mm, 0.6 shell diameter. Penial papilla-ejaculatory-pore position central. Penis terminal swelling conspicuous, terminal-bulb width 1.3 pre-bulb width. Penial gland absent. Base of FPSC (fertilization pouch-seminal receptacle complex) undetectable. Ducted gland on base of FPSC absent. Body-and-tube shape of FPSC: upper body folded right and downward, apex-plus-tube an up-pointed "V."



Explanation of Figures 20–25

Shells of other small Mahermana-Ilapiry-Vasiha caenogastropods. Figures 20–21. *Cyathopoma randalana*, Emberton & Pearce, sp. nov., representatives from Mounts Mahermana (Figure 20) and Ilapiry (Figure 21). Figure 22. *Malarinia calcopercula* Emberton, 1994, representative from Mount Ilapiry. Figure 23. *Tropidophora (Ligatella) vallorzi* Fischer-Piette, Blanc, Blanc & Salvat, 1993, representative from Mount Vasiha. Figure 24. *Omphalotropis vohimenae* Emberton & Pearce, sp. nov., holotype. Figure 25. *Omphalotropis costulata* Emberton & Pearce, sp. nov., holotype. All scale bars 1 mm.



Explanation of Figures 26–31

Some reproductive characters (Table 1) used in descriptions, as shown on stylized penis (Figure 26) and five types of FPSC (fertilization pouch-seminal receptacle complex; Figures 27–31). Abbreviations: b, base (glandular) of FPSC; d, body of FPSC; e, ejaculatory pore of penis; g, gland of FPSC; gd, ducted gland of FPSC; p-s, pre-swelling width of penis; pg, penial gland; pp, penial papilla; s, swelling width of penis; t, tube of FPSC. Stylized FPSCs: Figure 27, *Boucardicus rakotoarisoni* Emberton & Pearce, sp. nov.; Figure 28, *B. albocinctus*; Figure 29, *B. esetrae* Emberton & Pearce, sp. nov.; Figure 30, *B. divei*; Figure 31, *Cyathopoma randalana* Emberton & Pearce, sp. nov.

Local distribution: All three mountains, 100–700 m elevation.

Etymology: Also for Roger Randalana, in grateful recognition of his unflagging assistance throughout the Tolagnaro project.

Genus *Hainesia* Pfeiffer, 1856

Hainesia crocea (Sowerby, 1847)

Family DIPLOMMATINIDAE

Genus *Malarinia* Haas, 1961

Malarinia calcopercula Emberton, 1994

(Figure 22)

Malarinia sp. 1, Emberton et al., 1996:210. Emberton, 1997: 1147.

Representative: MBI 380.01DR (ad).

Other specimens: None.

Description of representative shell:

Size and Shape. Shell dextral. Diameter 2.2 mm; height 4.6 mm. Height-diameter ratio 2.1. Whorls 5.5. Spire angle 35 degrees. Apex angle 50 degrees. Spire profile convexity (outward departure from a straight line tangent to whorls n-0.5 and about the second whorl); 11% of shell diameter. Whorl periphery round. Suture depth one half whorl from aperture is 6% of shell diameter. Umbilicus before change in body whorl growth direction 3% of shell diameter. Final umbilicus 6% of shell diameter. Coiling tightness (whorl number divided by natural logarithm of shell diameter) 7.0.

Aperture. Aperture width (inside dimension, parallel to a line between the columellar and upper peristome insertions) 49% of shell diameter. Aperture height-width ratio (inside dimension, height measured to and perpendicular to a line between the columellar and upper peristome insertions) 1.00. Distance between columellar and upper peristome insertions is 41% of aperture width. Penultimate whorl not projecting into body whorl. Columella not truncate. Columellar plica absent. Columella slightly reflected. Apertural plane inclined downward; 5 degrees from rotational axis. Aperture shape sub-circular. Peristome expanded and thickened internally; second, internal peristome present, projecting less than 0.01 whorl. Change in growth direction of body whorl; occurs 0.1 whorls behind aperture. Apertural dentition absent.

Apex. First whorl diameter 0.7 mm. First two whorls diameter 1.0 mm. Embryonic whorls eroded.

Post-Embryonic Shell Sculpture and Color. Post-embryonic shell with regularly spaced transverse ribs on lower half of penultimate whorl, becoming weak to absent on body whorl. Basic shell color light yellow-brown.

Shell variation: No conspicuous difference in size or shape from the holotype.

Reproductive characters: Unknown.

Distribution: Previously known only from Vato Vavy and Vato Lahy summits near Mananjary, ca. 500 m elevation (Emberton, 1994). This record from Mt. Ilapiry, 300 m elevation, is an extreme, southward range extension.

Superfamily LITTORINOIDEA

Family POMATIASIDAE

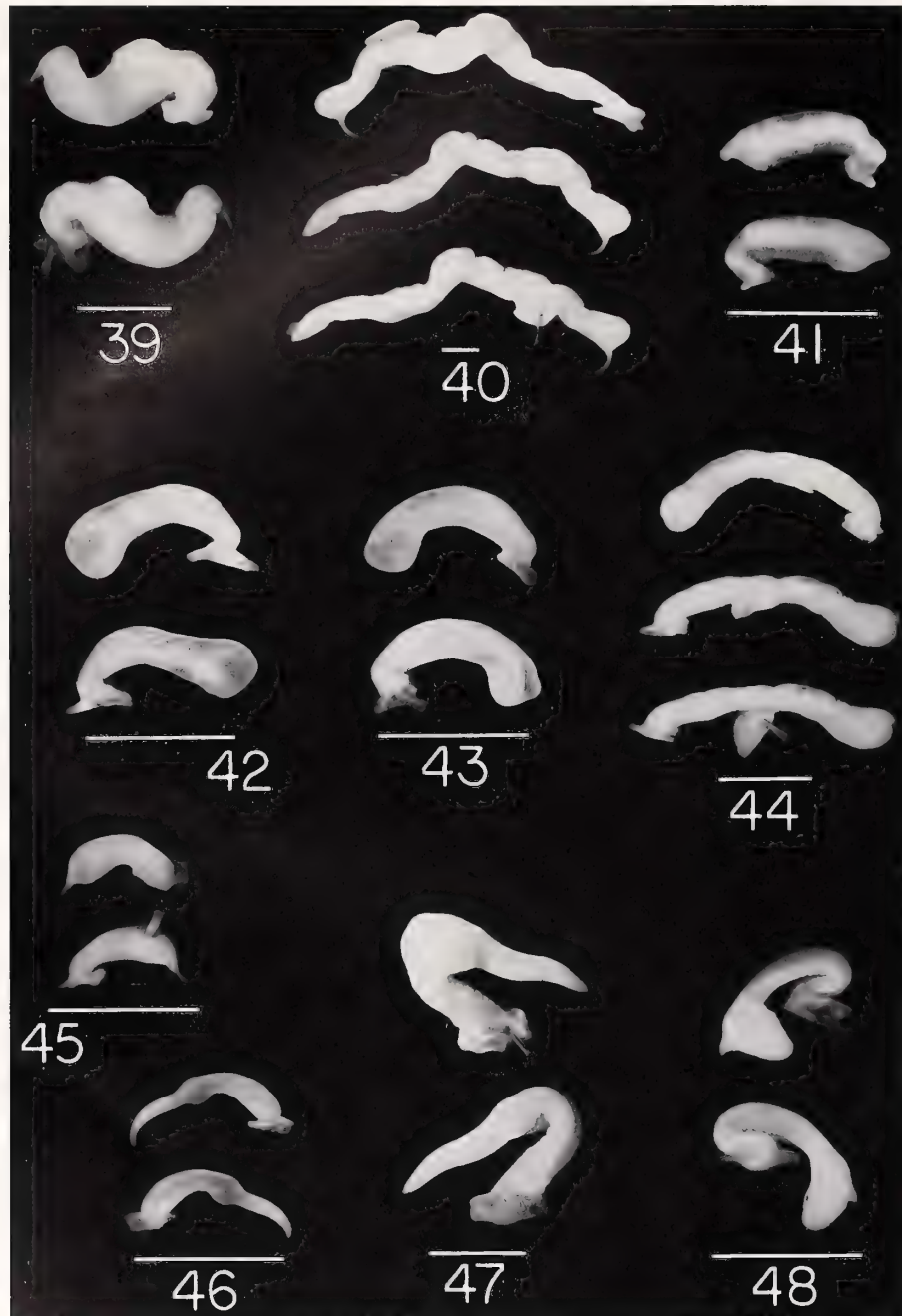
Genus *Tropidophora* Troschel, 1847

The large *Tropidophora* of Madagascar are currently in a taxonomic disorder that probably cannot be resolved without biochemical investigation (Emberton, 1995).



Explanation of Figures 32–38

Penes of Maherimana-Ilapiry-Vasiha *Boucardicus*. Figure 32. three stages in the dissection of a male to remove the penis (demonstrated on *Boucardicus albocinctus* [Smith, 1893]). Figure 33. *Boucardicus esetrae* Emberton & Pearce, sp. nov. Figure 34. *Boucardicus antiquus* Emberton & Pearce, sp. nov. Figure 35. *Boucardicus delicatus* Emberton & Pearce, sp. nov. Figure 36. *Boucardicus curvifolius* Emberton & Pearce, sp. nov. Figures 37–38. *Boucardicus albocinctus* (Smith, 1893): Figure 37, normal; Figure 38, mating. All scale bars 1 mm.



Explanation of Figures 39–48

Penes of Mahermana-Ilapiry-Vasiha *Boucardicus* and other small caenogastropods. Figure 39. *Boucardicus divei* Piette, Blanc, Blanc & Salvat, 1993. Figure 40. *Boucardicus culminans* Fischer-Piette, Blanc, Blanc & Salvat, 1993. Figure 41. *Boucardicus tridentatus* Emberton & Pearce, sp. nov. Figures 42–43. *Boucardicus rakotoarisoni* Emberton & Pearce, sp. nov., specimens from two populations. Figure 44. *Boucardicus mahermanae* Emberton & Pearce, sp. nov. Figure 45. *Boucardicus carylae* Emberton & Pearce, sp. nov. Figure 46. *Cyathopoma randalana* Emberton & Pearce, sp. nov. Figure 47. *Tropidophora (Ligatella) vallorzi* Fischer-Piette, Blanc, Blanc & Salvat, 1993. Figure 48. *Omphalotropis costulata* Emberton & Pearce, sp. nov. All scale bars 1 mm.

Tropidophora sp. 1*Tropidophora* sp. 2

Tropidophora (Ligatella) vallorzi Fischer-Piette,
Blanc, Blanc & Salvat, 1993

(Figures 23, 47, 68)

Tropidophora sp. 1, Emberton et al., 1996:210. Emberton,
1997:1146, 1149.

Representative: MBI 384.01DR (ad).

Other specimens: MBI 373.16D (3 ad, 9 juv), MBI 373.16A (2 ad, 7 juv), MBI 374.12D (4 juv), MBI 374.12A (3 ad, 2 juv), MBI 375.10D (2 ad, 9 juv), MBI 375.10A (3 ad, 3 juv), MBI 376.08D (3 ad, 11 juv), MBI 376.08A (1 ad, 4 juv), MBI 377.10D (2 ad, 7 juv), MBI 377.10A (3 juv), MBI 378.12D (12 juv), MBI 378.12A (1 ad, 7 juv), MBI 379.13D (6 ad, 13 juv), MBI 379.13A (4 juv), MBI 380.11D (3 ad, 15 juv), MBI 380.11A (11 juv), MBI 381.08D (3 ad, 20 juv), MBI 381.08A (2 ad [1 dissected], 18 juv), MBI 382.11D (1 juv), MBI 382.11A (2 juv), MBI 383.08D (4 ad, 17 juv), MBI 383.08A (4 juv), MBI 384.01D (6 ad, 21 juv; AMS C.203434 [1 ad]; MNHN [1 ad]; ANSP 400828 [1 ad]), MBI 384.01A (1 ad [dissected], 5 juv), MBI 385.05D (2 ad, 11 juv), MBI 385.05A (2 juv), MBI 386.08D (3 ad, 6 juv), MBI 386.08A (1 ad), MBI 387.05D (1 ad, 15 juv), MBI 387.05A (1 ad), MBI 388.03D (3 ad, 5 juv), MBI 391.01D (1 juv).

Description of representative shell:

Size and Shape. Shell dextral. Diameter 10.9 mm; height 12.2 mm. Height-diameter ratio 1.1. Whorls 4.9. Spire angle 70 degrees. Apex angle 70 degrees. Spire profile straight. Whorl periphery round. Suture depth one half whorl from aperture is 5% of shell diameter. Final umbilicus 8% of shell diameter. Coiling tightness (whorl number divided by natural logarithm of shell diameter) 2.0.

Aperture. Aperture width (inside dimension, parallel to a line between the columellar and upper peristome insertions) 47% of shell diameter. Aperture height-width ratio (inside dimension, height measured to and perpendicular to a line between the columellar and upper peristome insertions) 1.00. Distance between columellar and upper peristome insertions is 12% of aperture width. Penultimate whorl not projecting into body whorl. Columella not truncate. Columellar plica absent. Columella slightly reflected. Apertural plane inclined downward; 5 degrees from rotational axis. Aperture shape circular. Peristome reflected; no second, internal peristome. Ratio of aperture width including peristome to aperture width excluding peristome 1.2. No change in growth direction of body whorl near aperture. Apertural dentition absent.

Apex. First whorl diameter 1.4 mm. First two whorls diameter 2.2 mm. Embryonic whorls smooth.

Post-Embryonic Shell Sculpture and Color. Post-embryonic shell with four strong interrupted spiral ridges between sutures, white where they are strong, brown on both sides and where they are interrupted; with one weaker white spiral ridge between each stronger ridge on penultimate whorl, spiral ridges becoming more numerous on body whorl; sculpture continues on shell base and into umbilicus; frequent regular interruptions of spiral sculpture across the whorl extend as small ribs into the suture, and coincide with interruptions on the strong spiral ridges. Basic shell color light yellow-brown. Peristome (excluding periostracum) white with dark brown.

Shell variation: Most stations show a great dichotomy in size, presumably between males and females, as has been demonstrated for other *Tropidophora* (Emberton, 1995). The largest specimen reported here (station MBI 378) has 4.9 whorls, a diameter of 13.4 mm, and height of 14.8 mm. This specimen is also a uniform cream color, without darker color bands.

Description of reproductive characters (MBI 384.01A: 1 male; MBI 381.08A: 1 female): Penis length 5.2 mm, 0.5 shell diameter. Penial papilla-ejaculatory-pore position central. Penial papilla terminal, extremely strong protrusion, anteriorly directed. Penis terminal swelling slight. Penial gland absent. Base of FPSC (fertilization pouch-seminal receptacle complex) narrow-based, with multiple, internal apical lobes. Ducted gland on base of FPSC absent. Muscular funnel within body of FPSC apparently absent. Body-and-tube shape of FPSC: body-plus-tube sinuous, forming six loose, evenly spaced, "U" to "V" shaped bends.

Distribution: Described from the Anosy chain, Analava forest, and Ste. Luce forest (all north of Ft. Dauphin) (Fischer-Piette et al., 1993). Common throughout our samples on all three mountains, throughout all elevations (100–860 m).

Comments: It seems likely that *Tropidophora (Ligatella) maignei* Fischer-Piette, Blanc, Blanc & Salvat, 1993, is a synonym of this species.

Superfamily RISSOOIDEA

Family ASSIMINEIDAE

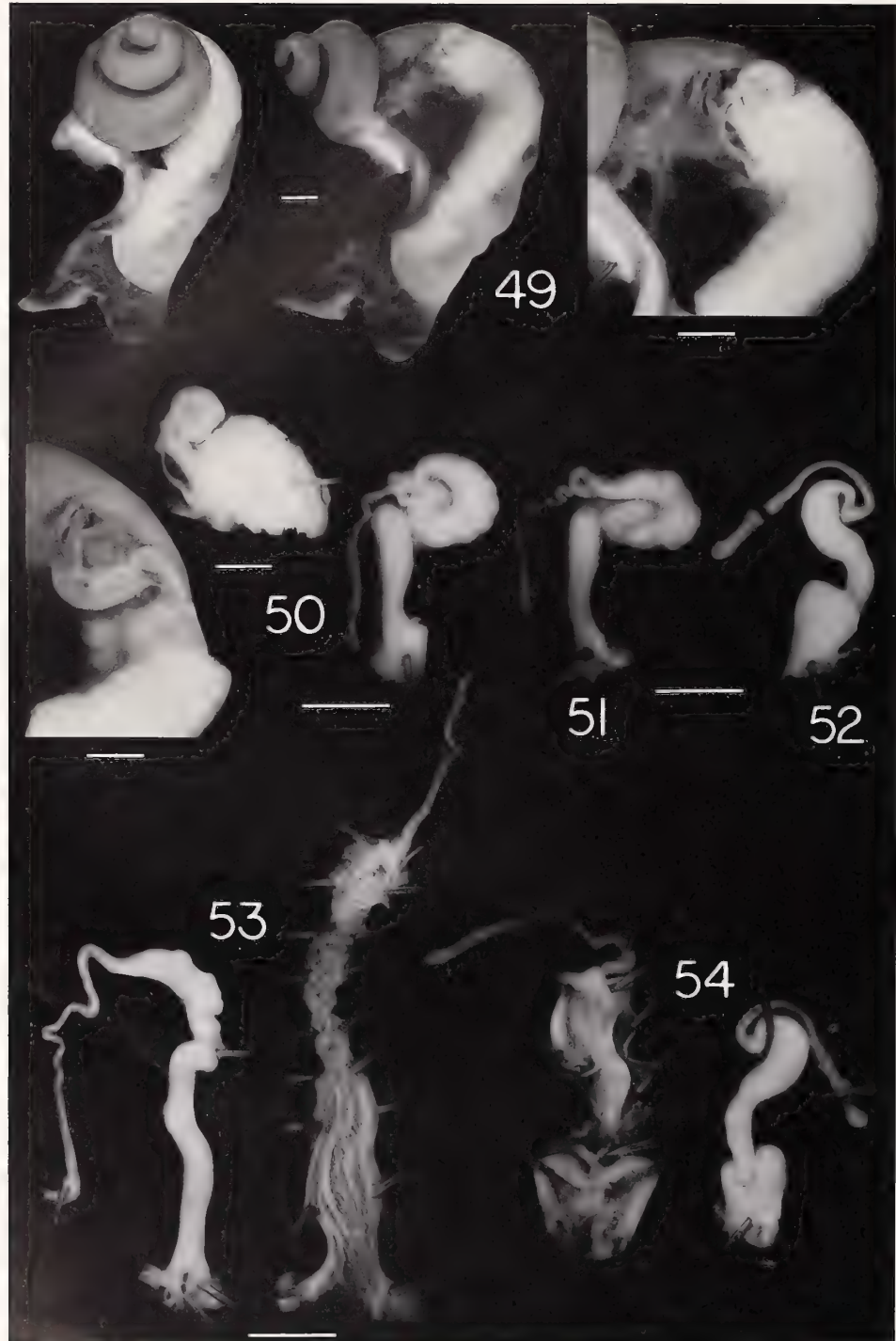
Genus *Omphalotropis* Pfeiffer, 1851

Omphalotropis vohimenae Emberton & Pearce,
sp. nov.

(Figure 24)

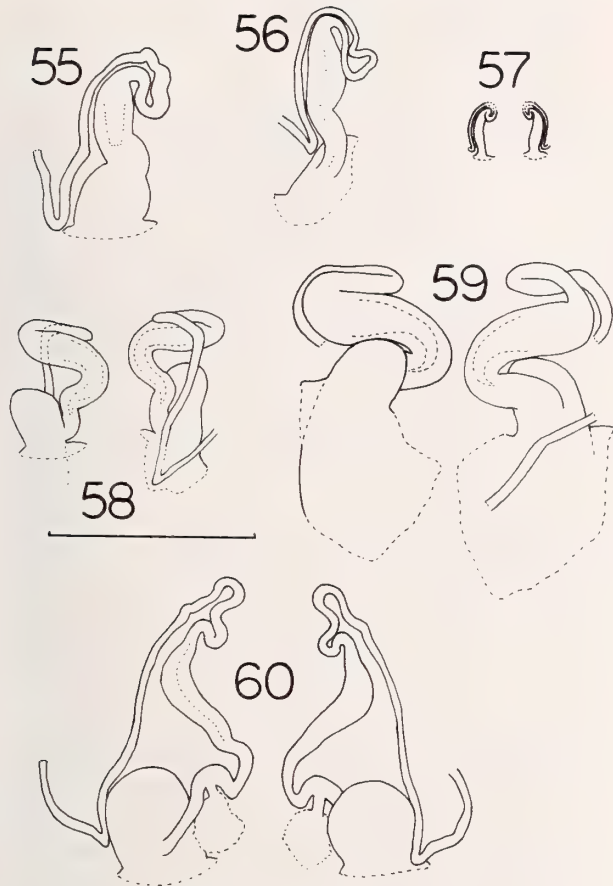
Omphalotropis sp. 1, Emberton et al., 1996:210. Emberton,
1997:1147.

Holotype: USNM 860790 (ex MBI 375.01DH, adult shell).



Explanation of Figures 49–54

FPSCs of Mahermana-Ilapiry-Vasiha *Boucardicus*. Figures 49, 50. Stages in the dissection of a female to remove and clean the FPSC (demonstrated on *Boucardicus albocinctus* [Smith, 1893]). Figures 51 and (stretched and dissected open) 53. Another *Boucardicus albocinctus* (Smith, 1893), mating. Figures 52 and (stretched and dissected open) 54. *Boucardicus culminans* Fischer-Piette, Blanc, Blanc & Salvat, 1993. All scale bars 1 mm.



Explanation of Figures 55–60

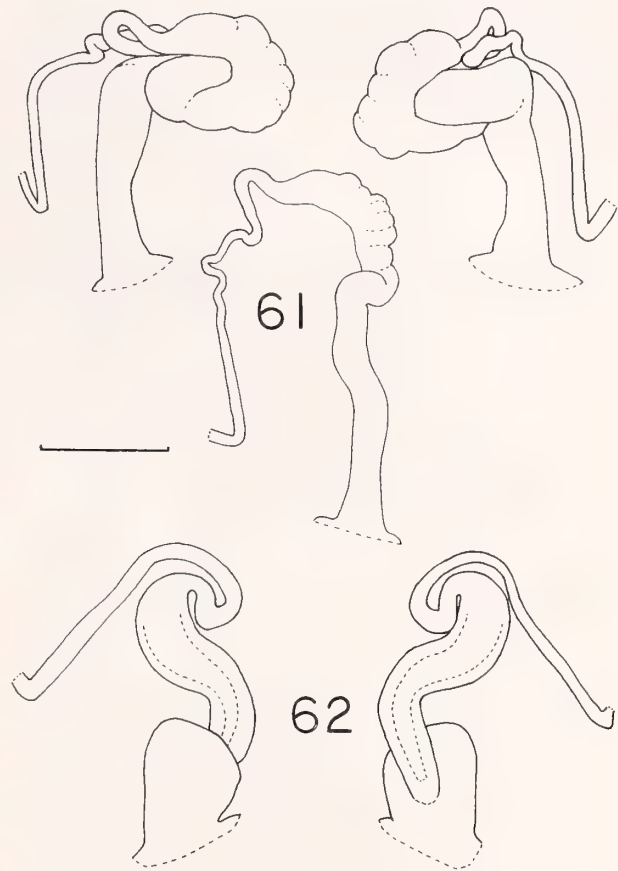
FPSCs of Mahermana-Ilapiry-Vasiha *Boucardicus*. Figure 55. *Boucardicus esetrae* Emberton & Pearce, sp. nov. Figure 56. *Boucardicus antiquus* Emberton & Pearce, sp. nov. Figure 57. *Boucardicus delicatus* Emberton & Pearce, sp. nov. Figure 58. *Boucardicus curvifolius* Emberton & Pearce, sp. nov. Figure 59. *Boucardicus victorhernandezii* Emberton, 1998. Figure 60. *Boucardicus divei* Fischer-Piette, Blanc, Blanc & Salvat, 1993. All to the same scale; scale bar 1 mm.

Paratypes: MBI 376.09DP (2 juv; AMS C.203435 [1 ad]), MBI 376.09AP (1 ad, 2 juv).

Type locality: Madagascar: Tulear Province: north of Fort Dauphin: northeast of village of Esetra: W-facing slope of Mount Mahermana, 200 m elevation: latitude 24°26'15"S, longitude 47°13'04"E: primary rainforest.

Description of holotype shell:

Size and Shape. Shell dextral. Diameter 2.6 mm; height 3.6 mm. Height-diameter ratio 1.4. Whorls 5.2. Spire angle 60 degrees. Apex angle 60 degrees. Spire profile straight. Whorl periphery rounded to slightly angular, pre-sutural ridge present. Suture depth one half whorl from aperture is 5% of shell diameter. Final umbilicus 14% of

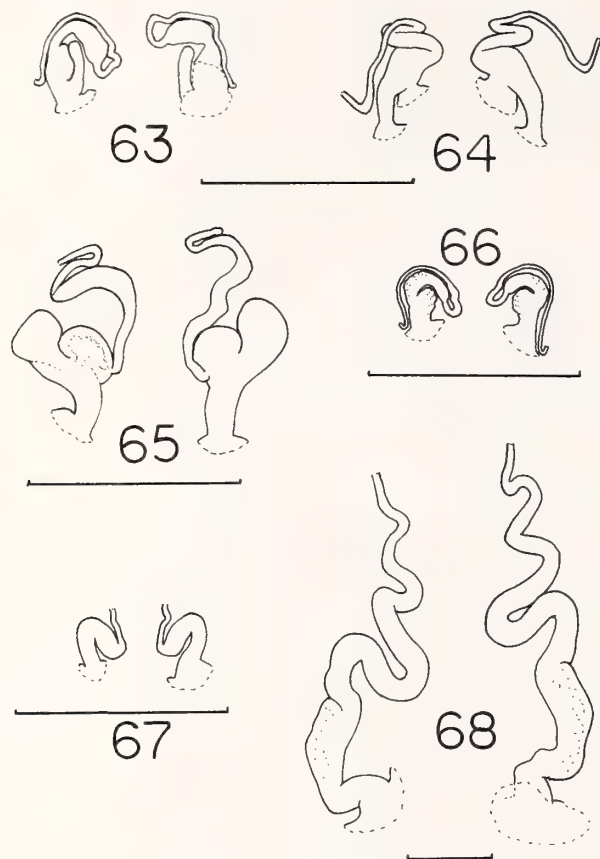


Explanation of Figures 61 and 62

FPSCs of Mahermana-Ilapiry-Vasiha *Boucardicus*. Figure 61. *Boucardicus albocinctus* (Smith, 1893). Figure 62. *Boucardicus culminans* Fischer-Piette, Blanc, Blanc & Salvat, 1993. Line drawings of same specimens photographed in Figure 35. To same scale; scale bar 1 mm.

shell diameter. Coiling tightness (whorl number divided by natural logarithm of shell diameter) 5.4.

Aperture. Aperture width (inside dimension, parallel to a line between the columellar and upper peristome insertions) 50% of shell diameter. Aperture height-width ratio (inside dimension, height measured to and perpendicular to a line between the columellar and upper peristome insertions) 0.85. Distance between columellar and upper peristome insertions is 54% of aperture width. Penultimate whorl projecting into body whorl. Occupying 2% of aperture height measure. Columella not truncate. Columellar plica absent. Columella slightly reflected. Apertural plane inclined downward; 15 degrees from rotational axis. Aperture shape ovate. Peristome simple; no second, internal peristome. Change in growth direction of body whorl; occurs 0.1 whorls behind aperture. Apertural dentition absent.



Explanation of Figures 63–68

FPSCs of Mahermana-Ilapiry-Vasiha *Boucardicus* and other small caenogastropods. Figure 63. *Boucardicus tridentatus* Emberton & Pearce, sp. nov. Figure 64. *Boucardicus rakotoarisoni* Emberton & Pearce, sp. nov. Figure 65. *Boucardicus mahermanae* Emberton & Pearce, sp. nov. Figure 66. *Boucardicus carylae* Emberton & Pearce, sp. nov. Figure 67. *Cyathopoma randalana* Emberton & Pearce, sp. nov. Figure 68. *Tropidophora (Ligatella) vallorzi* Fischer-Piette, Blanc, Blanc & Salvat, 1993. All scale bars 1 mm.

Apex. First whorl diameter 0.4 mm. First two whorls diameter 0.7 mm. Embryonic whorls smooth.

Post-Embryonic Shell Sculpture and Color. Post-embryonic shell with strong transverse ribs on the whorl shoulder only, lower part of whorl with extremely fine transverse rows of punctae; strong peripheral keel on the body whorl appears as a super-sutural spiral ridge on earlier whorls; another spiral ridge on the most basal part of the shell base. Basic shell color pale tan.

Shell comparisons: Unique within the genus for its partial, subsutural rib sculpture.

Reproductive characters: Unknown.

Local distribution: Known only from Mt. Mahermana, 100–200 m elevation.

Etymology: For the Vohimena Mountain Chain, north of Fort Dauphin.

Omphalotropis costulata Emberton & Pearce,
sp. nov.

(Figures 25, 48)

Omphalotropis sp. 2, Emberton et al., 1996:210. Emberton, 1997:1147.

Holotype: USNM 860791 (ex MBI 381.03DH, adult shell).

Paratypes: MBI 378.21AP (1 ad [dissected]), MBI 379.14DP (1 juv; AMS C.203436 [1 ad]), MBI 379.14AP (1 ad), MBI 381.03DP (1 ad), MBI 381.03AP (3 ad).

Type locality: Madagascar: Tulear Province: north of Fort Dauphin: west of village of Mahialambo: east-south-east-facing slope of Mount Ilapiry, 200 m elevation: latitude 24°51'39"S, longitude 47°00'46"E: primary rainforest.

Description of holotype shell:

Size and Shape. Shell dextral. Diameter 2.4 mm; height 3.3 mm. Height-diameter ratio 1.4. Whorls 4.7. Spire angle 55 degrees. Apex angle 55 degrees. Spire profile straight. Whorl periphery rounded to slightly angular, pre-sutural ridge present. Suture depth one half whorl from aperture is 5% of shell diameter. Final umbilicus 14% of shell diameter. Coiling tightness (whorl number divided by natural logarithm of shell diameter) 5.4.

Aperture. Aperture width (inside dimension, parallel to a line between the columellar and upper peristome insertions) 53% of shell diameter. Aperture height-width ratio (inside dimension, height measured to and perpendicular to a line between the columellar and upper peristome insertions) 0.84. Distance between columellar and upper peristome insertions is 50% of aperture width. Penultimate whorl projecting into body whorl. Occupying 4% of aperture height measure. Columella not truncate. Columellar plica absent. Columella slightly reflected. Apertural plane inclined downward; 10 degrees from rotational axis. Aperture shape ovate. Peristome simple; no second, internal peristome. Change in growth direction of body whorl; occurs 0.1 whorls behind aperture. Apertural dentition absent.

Apex. Embryonic whorls 2.0; diameter 0.8 mm. First whorl diameter 0.5 mm. First two whorls diameter 0.8 mm. Embryonic whorls with weak transverse ribs.

Post-Embryonic Shell Sculpture and Color. Post-embryonic shell with strong regular transverse ribs; strong peripheral keel on the body whorl appears as a super-sutural spiral ridge on earlier whorls; another spiral ridge

on the most basal part of the shell base. Basic shell color pale yellow-orange.

Shell variation: No conspicuous variation in size or shape.

Shell comparisons: Unique in the genus for its transverse rib sculpture.

Description of reproductive characters (MBI 378.21AP: 1 male): Penis length 1.5 mm, 0.6 shell diameter. Penial papilla-ejaculatory-pore position dorsal. Penial dorsal papilla subterminal. Penis terminal swelling extreme, terminal-bulb width approximately 3.5 pre-bulb width. Penial gland absent. FPSC (fertilization pouch-seminal receptacle complex) unknown.

Local distribution: Known only from Mt. Ilapiry, 200–500 m elevation.

Etymology: For the sculpture of transverse ribs (*L. costulata*).

BOUCARDICUS CONSERVATION STATUSES

Analyses of individual species are given above in the species descriptions. To summarize, all 17 *Boucardicus* species are proposed as either Vulnerable, Endangered, or Critically Endangered. The following four species should be listed as **Critically Endangered**: *B. fidimananai* sp. nov., *B. fortistriatus* sp. nov., *B. randalanai* sp. nov., and *B. simplex* sp. nov. The 12 species that should be listed as **Endangered** are: *B. carylae* sp. nov., *B. culminans*, *B. curvifolius* sp. nov., *B. delicatus* sp. nov., *B. divei*, *B. esetrae* sp. nov., *B. magnilobatus* sp. nov., *B. maher-manae* sp. nov., *B. rakotoarisoni* sp. nov., *B. simplex* sp. nov., *B. tridentatus* sp. nov., and *B. victorhernandezi*. Two additional species qualify as **Vulnerable**: *B. albocinctus* and *B. antiquus*.

DISCUSSION

These descriptions of 22 small caenogastropod species support our previous distributional and ecological analyses of Mahermana-Ilapiry-Vasiha land snails (Emberton et al., 1996, 1999; Emberton, 1997). In preparation are three additional papers describing Mahermana-Ilapiry-Vasiha small pulmonates.

The DELTA system (Dallwitz et al., 1993a, b) proved useful not only in reducing the tedium and possible transcription errors involved in manually writing descriptions, but also in enforcing rigor and consistency in defining and scoring characters.

Nothing is known of the life history or autecology of any of these environmentally threatened animals.

Acknowledgments. We are grateful to the U.S. National Science Foundation and USAID for funding (grant DEB-9201060 to K.C.E.); to staffs of the Ranomafana National Park Project, the Madagascar Département des Eaux et Forêts, and the Tolagnaro

(Fort Dauphin) office of the World Wide Fund for Nature for logistical aid; to Roger Randalana and assistants from Esetra, Mahialambo, and Malio for collecting; to Felix Rakotomalala for curatorial assistance; and to Lucia Emberton for help in mounting the photographs.

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Bequaert, J. C. & W. B. Miller. 1973. *The Mollusks of the Arid Southwest*. University of Arizona Press: Tucson. xvi + 271 pp.

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Feder, H. M. 1980. Asteroidea: the sea stars. Pp. 117–135 in R. H. Morris, D. P. Abbott & E. C. Haderlie (eds.), *Intertidal Invertebrates of California*. Stanford University Press: Stanford, Calif.

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